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Reduced herbivore resistance in introduced smooth cordgrass (*Spartina alterniflora*) after a century of herbivore-free growth

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Abstract We compared resistance to insect herbivory in two introduced populations of smooth cordgrass (*Spartina alterniflora*) differing in their history of herbivory. One population in Willapa Bay, Washington, has spread in the absence of herbivory for more than a century, while another population in San Francisco, California, was introduced 20 years ago and is fed upon by the *Spartina*-specialist planthopper, *Prokelisia marginata*. The planthopper is a sap-feeder common on the Atlantic and Gulf coasts of North America, where smooth cordgrass is native. Smooth cordgrass plants from Willapa Bay (WB), San Francisco Bay (SFB), and Maryland (the source of the SFB introduction) were exposed to *P. marginata* herbivory over two consecutive summers in a common greenhouse environment, and their growth was compared with that of control plants that were grown herbivore-free. The planthoppers had relatively little effect on the growth of SFB plants, with plants exposed to herbivores averaging 77% and 83% of the aboveground biomass of herbivore-free controls after the first and second season of herbivory, respectively. The growth of plants from Maryland was similarly little-affected by the planthoppers, with the plants exposed to herbivores averaging near 100% of the biomass of herbivore-free controls after two seasons. In contrast, the growth of the WB plants was greatly reduced by the planthopper, with the plants exposed to planthopper herbivory averaging only 30% and 12% of the aboveground biomass of herbivore-free controls after the first and second seasons of herbivory, respectively. By the end of the second season of herbivory, 37% of the WB plants exposed to herbivory had died, while none of the SFB plants exposed to herbivores had died. Among WB clones, there was variation in resistance; one WB clone suffered 0% mortality while another suffered 100% mortality when exposed to herbi-

vores. Short-term herbivory experiments with the putative founder clone for the WB population suggested that the WB founder was similar to the more resistant WB clones in its susceptibility to planthopper herbivory. Nitrogen analyses of green leaf tissue indicated that WB plants, including the WB founder clone, averaged 70% more total leaf nitrogen than SFB and Maryland plants. In a planthopper choice experiment, more planthoppers were observed on WB plants than SFB plants after 95 days of exposure to herbivory. Planthopper preference for WB plants may have contributed to the lower resistance of WB plants to herbivory; however, even before planthoppers had become more abundant on the WB plants, the proportion of leaves with 50% or more dead tissue averaged significantly greater on the WB plants, suggesting a difference between populations in tolerance to herbivory as well. Multiple factors, including a founder effect, further loss of herbivore tolerance, and herbivore preference for WB plants, appear to account for the reduced planthopper resistance in the WB population.

Key words Herbivore resistance · Herbivore tolerance · Herbivore preference · Founder effect · Invasive plants

Introduction

Founder effects, genetic drift, and natural selection can all lead to genetic differentiation in populations of an invading species, relative to the invader's source population. Genetic differences between introduced populations and putative native source populations of plant species have been reported at the level of allozymes (Schwaegerle and Schaal 1979; Brown and Marshall 1981; Barrett and Shore 1989; Rejmanek et al. 1991; Novak and Mack 1993), DNA markers (Rejmanek et al. 1991), phenotypic traits (Wagner 1983; Glover and Barrett 1987; Olivieri et al. 1991), and mating systems (Glover and Barrett 1986; Bailey 1994), but genetic differentiation for specific ecological traits important in interspecific interactions has rarely been investigated in introduced plant

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populations (but see Jain and Martins 1979; Olivieri 1984; Blossey and Notzöld 1995). An ecological character of particular interest in introduced plant populations is response to herbivory. Because many introduced plant species invade new geographic sites that lack many or all of their native insect herbivores (DeBach and Rosen 1991), there is the possibility that a population freed from herbivory might lose adaptations to herbivory over time (Janzen 1975), as has been suggested for some grass populations that were excluded from mammalian grazing pressures for several decades (Painter et al. 1989) and purple loosestrife introduced to the United States from Europe (Blossey and Notzöld 1995). In this study, we tested for genetic differentiation with respect to herbivore resistance between two introduced Pacific populations of smooth cordgrass (*Spartina alterniflora*) with differing histories of herbivory at their sites of invasion.

Smooth cordgrass, a 1- to 2-m-tall perennial salt-marsh grass native to the Atlantic and Gulf Coasts of North America, is presently invading open-mud intertidal habitats in both Willapa Bay, Washington and San Francisco Bay, California. In Willapa Bay, smooth cordgrass was introduced in 1894 with oyster shipments from either the New York City area or Chesapeake Bay (Sayce 1988); the founding propagule may have consisted of a single clone. This putative founding clone, identified as a homogeneous circular patch from early aerial photographs, still survives today at its original site of establishment (Stiller and Denton 1995). A comparison of DNA markers between the putative founding clone and other plants in Willapa Bay suggested that all plants were descendants of the putative founding clone, although the descendants were not all genetically identical due to sexual recombination in this hexaploid species (Stiller and Denton 1995). Over the past century, smooth cordgrass in Willapa Bay has spread to occupy over 1000 ha of open mud, growing in the absence of insect herbivores. In contrast, smooth cordgrass in San Francisco Bay is fed upon by the planthopper, *Prokelisia marginata* (Homoptera), a *Spartina* specialist that is also common where smooth cordgrass is native, along the Atlantic and Gulf Coasts of North America (Denno et al. 1980; Strong and Stiling 1983). The San Francisco Bay smooth cordgrass population was introduced in the mid-1970s via seeds from a native population in Maryland (Daehler and Strong 1994), and the planthopper was present in San Francisco Bay before the introduction of smooth cordgrass (Lane 1969).

In this study, we compared resistance to planthopper herbivory between the Willapa Bay smooth cordgrass population, which has not experienced insect herbivory for more than a century, and the San Francisco Bay and Maryland populations, which have historically been exposed to insect herbivory. The goals of our study were: (1) to test whether plants from Willapa Bay are less resistant to planthopper herbivory than plants from San Francisco Bay and Maryland; (2) to test planthopper preference as a possible mechanism responsible for differences in resistance between populations; and (3) to

address the possibility of a founder effect in the Willapa Bay population by comparing resistance in the putative Willapa Bay founder clone to that of other plants. Because smooth cordgrass in Pacific estuaries reduces native shorebird feeding habitats, threatens oystering grounds, and clogs flood control channels (Daehler and Strong 1996), we were also interested in implications of genetic differentiation among populations for the prospects of biological control of this noxious invader.

Materials and methods

Measuring the effect of herbivores

Seeds of smooth cordgrass (*Spartina alterniflora*) were collected in fall 1992 from four sites spanning the plant's current distribution in Willapa Bay, Washington (Diamond Point, Leadbetter Point, Oysterville, and Palix River). Seeds from the San Francisco Bay population were collected from about 100 individual smooth cordgrass clones located near the species' original site of introduction at Coyote Hills Slough in south San Francisco Bay. All seeds were stored over winter in 50% sea water at 4°C and germinated in spring 1993. Five seedlings from each population were vegetatively propagated for herbivory experiments. The five seedlings from the San Francisco Bay population were randomly chosen, one from each of five different maternal plants, while the five Willapa Bay seedlings were also chosen randomly with the restriction that one seedling was chosen from each of the four collection sites (two from Diamond Point were used, for a total of five seedlings).

The seedlings were grown over summer 1993 and winter 1994 in 30x45x13 cm pans containing a mixture of 25% Bodega Bay intertidal mud and 75% vermiculite (by volume). These plants were housed together in a greenhouse at Bodega Bay in northern California. In March 1994, each plant was divided into 12 clonal replicates consisting of three to five shoots. We attempted to allocate equal root biomass to each replicate. These replicates were individually transferred to 2.8-l pots containing the same mixture of vermiculite and mud. Extra clonal replicates were also reserved for later use in the planthopper choice experiment. In fall 1993, smooth cordgrass seeds were obtained directly from a Maryland population (Environmental Concerns Inc., St. Michaels, Md.), and eight random seedlings that germinated in spring 1994 were transferred to 2.8-l pots for use in the herbivory experiment.

In May 1994, the aboveground biomass of each clonal replicate was estimated by measuring the length of all stems. Aboveground dry biomass is highly correlated with stem length in smooth cordgrass ($r=0.98$, Daehler and Strong 1995), allowing accurate, non-destructive estimates of aboveground biomass to be made from measurements of stem lengths. Within each clone, the 12 replicates were paired for equal size, and one replicate was randomly assigned to the herbivory treatment, while the other was deferred to the no-herbivory control group. The eight plants from Maryland were also paired by size and randomly assigned to the herbivory treatment or the no-herbivory control group. All plants were then transferred to a 2.5x3.5 m greenhouse that had been divided in half with a fine mesh fabric (American Agrifabrics Inc., Alpharetta, Ga.) that prevented most planthopper dispersal between sides. Each half of the greenhouse held a large water table containing 33% seawater, and all plants that had been assigned to the herbivory treatment were placed in the water table on one side of the greenhouse. The initial side to be used for the herbivory treatment was chosen randomly, and a total of approximately 300 adult planthoppers (*P. marginata*) collected from San Francisco Bay were evenly sown onto plants in the herbivory treatment. All pots in the herbivory treatment were in close proximity, allowing planthoppers to move freely from pot to pot within the herbivory treatment. The herbivore-free control plants were placed in the identical water table on the opposite side of the greenhouse.

Every week during the summer and every 2 weeks during the winter, the location of plants within each treatment was randomized to minimize position effects, while every 2 weeks (every 3–4 weeks in the winter), the side of the greenhouse used for the herbivory treatment was switched by moving all plants in the herbivory treatment (and their associated planthoppers) to the opposite side of the greenhouse and placing the no-herbivory plants where the herbivory treatment had been. Throughout the summer, the water tables were maintained with approximately 4 cm of standing water by adding fresh water as needed, and every 4 weeks, 32 g Plantex 20-20-20 fertilizer dissolved in water was added to each water table. Over the summer, completely dead, shedding leaves (usually the oldest leaves) were removed by hand, simulating the natural removal of dead leaves by tidal action under field conditions and allowing natural growth of the plants. Every few weeks, we counted the number of planthoppers on three to five plants to obtain rough estimates of planthopper densities in the herbivory treatment over time. Planthoppers occasionally found on plants in the no-herbivory treatment were removed by hand, and planthopper densities on the no-herbivory treatment always averaged fewer than one planthopper per two plants. With this experimental design, each plant pair is treated as a replicate, since plants making up pairs were identified before the start of the experiment, and rotation was applied to all pairs in the same fashion (C. M. Drake, personal communication).

In mid-October 1994, the aboveground biomass of all plants was estimated by measuring the length of all stems and shoots. The planthoppers were then removed by spraying each plant with a watering hose outside the greenhouse. The herbivore-free control plants were also sprayed with water. This October herbivore removal simulated a natural die-back of the planthopper population that occurs over winter in the field (Roderick 1987; Daehler and Strong 1995).

In mid-April 1995, the stems of all plants were again measured to estimate combined over-winter and early spring growth. Approximately 300 adult planthoppers were then added to the herbivory treatment, simulating the pulse in the planthopper population that occurs in the field in spring (Roderick 1987; Daehler and Strong 1995). As in 1994, the herbivory treatment plants were exposed to planthopper herbivory from April until late September 1995. All stems and shoots from all plants were then harvested and dried to a constant mass at 55°C to determine final biomass.

Throughout the experiment, plants in the greenhouse were exposed to natural sunlight, and large open vents at the sides and top of the greenhouse provided a semi-open-air environment. Greenhouse temperatures averaged around 23°C by day and 12°C by night in the summers. Winter temperatures averaged about 2°C lower, both day and night. On two sunny summer days, temperatures in the greenhouse peaked at 33°C, while on the coldest winter nights, temperatures dropped as low as 3°C. This range of temperatures is similar to that in both San Francisco and Willapa Bays (National Ocean Service 1994), although peak summer temperatures in both Willapa Bay and San Francisco Bay exceeded those in our greenhouse, and extreme low temperatures in Willapa Bay were lower than those in our greenhouse.

Impact of herbivory on the Willapa Bay founding clone

Clonal fragments dug from the putative founding clone (Stiller and Denton 1995) were obtained from K. Sayce (Willapa Bay, Wa.) in early April 1995 and grown out in greenhouse pans in the same mixture of intertidal mud and vermiculite used for the other plants. April was the earliest date that the putative founder clone could be sampled and shipped to us. After 3 months, the founder clone had grown sufficiently to be divided into ten clonal replicates. The clonal replicates consisted of two to five stems each and were transferred to 2.8-l pots. After 1 month of growth in the pots, the replicates were measured, paired by size, and added to the herbivory experiment, with one clonal replicate from each pair exposed to planthopper herbivory and the other kept herbivore-free. The herbivory treatment plants were exposed to the planthoppers for

8 weeks, from August through September and their aboveground biomass was then compared to that of the herbivore-free controls.

Planthopper choice experiment

In January 1995, extra clonal replicates from April 1994 were further divided in replicates containing five to seven stems each and transferred to 2.8-l pots. Aboveground biomass of the plants was estimated by measuring all stems in April, and ten plants from Willapa Bay (four different clones) were paired by size with ten plants from San Francisco Bay (five different clones). Pots were transferred to a small (2x2 m) greenhouse and plant pairs were placed in close proximity so that the leaves of plant pairs intermingled. In early May, each plant was inoculated with seven third- or fourth-instar planthopper nymphs, and the number of planthoppers on each plant was counted every 1–2 weeks over the summer to determine whether the planthoppers favored the Willapa Bay plants over the San Francisco Bay plants. The position of plant pairs in the greenhouse was rotated every week to minimize position effects, and each plant pair was fertilized every 4 weeks with 2 g of Plantex 20-20-20 dissolved in water. Individual planthopper feeding scars on leaves are usually difficult to score; however, collective feeding by multiple planthoppers can accelerate leaf senescence and kill tissue directly (C. C. Daehler, personal observation). As an estimate of the impact of herbivory, in late August we counted the proportion of leaves on each plant with 50% or more dead (brown) tissue. If a plant contained more than 100 leaves, only the first 100 leaves encountered were scored.

In early August 1995, six fresh Willapa Bay-San Francisco Bay plant pairs that had grown throughout the summer without herbivores were added to the herbivore choice experiment to determine whether planthopper preference differed in mid-summer. No planthoppers were placed on these fresh plants, rather they were positioned in pairs in close proximity to infested plants, and the planthoppers were allowed to colonize these plants naturally. Planthopper counts on these new plants were made from August through September.

Nitrogen analyses of leaf tissues

Green leaves from herbivory and herbivore-free plants that were harvested in early September 1995 were dried at 55°C, ground to a powder in an Alpine mill, passed through a #40 mesh and analyzed for total nitrogen content by the University of California Davis DANR Analytical Laboratory (Davis, Calif.) using a nitrogen gas analyzer (Sweeney 1989). Where possible, leaves from two replicate pots of each clone were analyzed separately from both the herbivory and herbivore-free treatments; however, for two of the five Willapa clones, leaves from herbivory treatment replicates had to be pooled to obtain sufficient material for analysis. Total nitrogen content was also measured from green leaves of all eight Maryland plants and four replicates of the Willapa founder clone.

Statistical analyses

All statistical analyses were conducted using Systat version 5.01 for Windows (Systat Inc., Evanston, Ill.). Differences between San Francisco Bay and Willapa Bay plants in resistance to herbivory were statistically analyzed using the difference between the logarithms of biomass of the herbivore-free plant and the herbivory treatment plant for each plant pair as the response variable. This measure has been employed in comparing the fitness of selfed and outcrossed progeny in studies of inbreeding depression (Johnston and Schoen 1994). As in analyses of population differences in inbreeding depression, it is the ratio between the biomass of the herbivory and herbivore-free plants that is of interest in comparing the response to herbivory between populations, not the absolute, scale-dependent differences in biomass between herbivory and herbivore-free plants (Johnston and Schoen 1994). The logarithm-

mic transformation makes the ratio between herbivory and herbivore-free plants additive in the ANOVA and thus appropriate for comparing populations and interpreting significant population effects in the ANOVA as differences in response to herbivory between the two populations (Johnston and Schoen 1994). In the ANOVA, biomass measurements were treated as repeated measures over time (fall 1994, spring 1995, and fall 1995), place of origin (San Francisco Bay or Willapa Bay) was treated as a fixed factor, and clone nested within origin was considered a random factor (Neter et al. 1990). Although differences in log-transformed biomasses were used for all statistical analyses, untransformed ratios between biomass of herbivory and herbivore-free plants are presented in the figures for their relative ease of interpretation.

For the planthopper choice experiment, differences in planthopper numbers on Willapa Bay versus San Francisco Bay plants were analyzed using ANOVA, with number of planthoppers counted on a plant at each census date as a repeated measure, plant origin as a fixed factor and plant pair as a random factor. Significant differences between Willapa Bay and San Francisco Bay plants at each census period were then tested for using univariate *F*-tests (Wilkinson 1992).

Differences in nitrogen content of leaf tissues were compared with analysis of variance using log-transformed values for nitrogen content to improve normality. Origin of the plant (San Francisco Bay, Willapa Bay, Willapa Bay founder, or Maryland) and herbivory treatment were both assigned as fixed factors in the ANOVA (Neter et al. 1990). All tests for significance based on ANOVAs used type III sums of squares (Wilkinson 1992).

Results

Herbivore loads

By May 1994, plants in the herbivory treatment averaged about 10 planthoppers per plant. Cohorts of eggs hatched almost synchronously approximately every 3 weeks, increasing the population over time. In June, planthopper densities averaged around 30 per plant and between July and August planthopper densities ranged from 50 to 100 per plant. By September, a few weeks before removal of the planthoppers, densities were estimated at above 200 per plant (mostly nymphs). The buildup of the planthopper population observed in the greenhouse over summer is also characteristic of planthopper populations in the field, and the densities of planthoppers in the greenhouse experiment were similar to densities that commonly occur in the field in San Francisco Bay (Daehler and Strong 1995). The greenhouse planthopper population densities in 1995 followed a similar pattern to that in 1994.

Growth response to herbivores

There was a highly significant effect of plant origin on growth response to herbivores (Table 1), reflecting a much greater impact of herbivores on Willapa Bay plants than on San Francisco Bay plants. The significant effect of clone nested within origin (Table 1) indicated variation among clones within each population in their response to herbivory (Figs. 1 and 2). A significant origin-by-time interaction was due to an increasing difference between the Willapa Bay plants and the San Francisco

Table 1 Repeated-measures analysis of variance on the difference between log-transformed biomasses of herbivore-free and herbivore-exposed plants. *Origin* is the place of plant origin (San Francisco or Willapa Bay). A significant effect of origin indicates a difference between Willapa Bay and San Francisco Bay populations in their response to herbivory. *Time* represents the time of biomass measurement (fall 1994, spring 1995, or fall 1995). Greenhouse-Geisser $\epsilon=0.86$; conclusions are not affected by Greenhouse-Geisser correction for non-sphericity

	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Between subjects				
Origin	1	51.17	36.11	<0.001
Clone (Origin)	7	1.42	2.55	0.03
Error	37	0.56		
Within subjects				
Time	2	4.30	10.0	<0.001
Time×Origin	2	4.70	10.9	<0.001
Time×Clone (Origin)	14	0.43	2.97	0.001
Error	74	0.15		

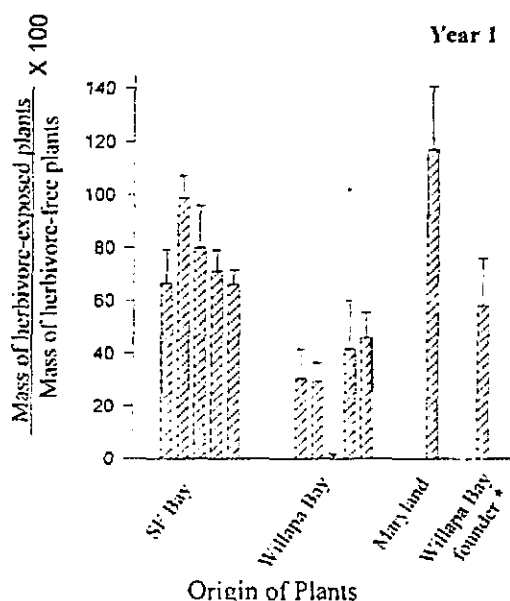


Fig. 1 Mass of herbivore-exposed plants relative to no-herbivory plants after one summer (22 weeks) of exposure to herbivory by the planthopper *Prokelisia marginata*. From left to right, the five bars in the San Francisco Bay population represent clones coy84, coy70, coy140, coy81, and coy106, while the five bars in the Willapa Bay population represent clones diam10, lead2, oyst10, palix5, and diam5. *The response of the Willapa Bay founder clone to 22 weeks of herbivory was estimated by linear extrapolation of the response to 8 weeks of herbivory (see Results). Error bars represent 1 SE

Bay plants in their response to herbivory over time. The longer the exposure to herbivory, the greater the difference between the response of the Willapa Bay and San Francisco Bay populations (Figs. 1 and 2).

All of the Willapa Bay clones were less resistant to herbivory than the San Francisco Bay clones (Fig. 2). At the end of the first season, San Francisco Bay herbivory plants averaged 77% of the biomass of herbivore-free plants, while Willapa Bay herbivory plants averaged only

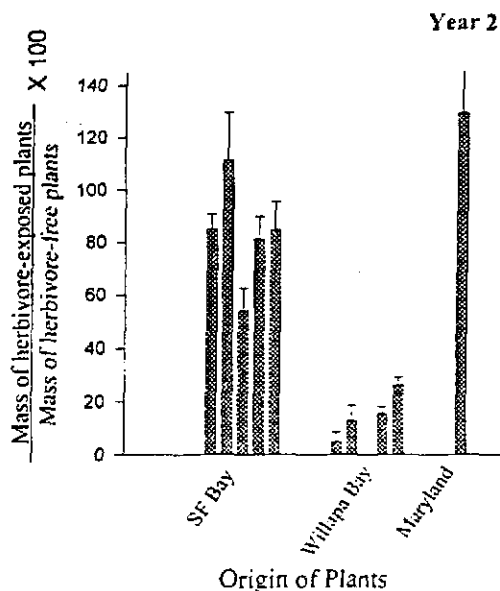


Fig. 2 Final mass of herbivory plants relative to non-herbivory plants after two summers of exposure to herbivory by the planthopper *P. marginata*. From left to right, the five bars in the San Francisco Bay population represent clones coy84, coy70, coy140, coy81, and coy106, while the five bars in the Willapa Bay population represent clones diam10, lead2, oyst10 (blank), palix5, and diam5. All plants in the oyst10 herbivory treatment died. Error bars represent 1 SE.

30% of the biomass of herbivore-free plants (Fig. 1). At the end of the second summer of herbivory, San Francisco Bay herbivory plants averaged 83% of the biomass of herbivore-free controls, while Willapa Bay herbivory plants averaged less than 20% of the biomass of herbivore-free controls (Fig. 2).

Between October 1994 and April 1995, all plants grew without herbivores, and San Francisco Bay plants increased in biomass by an average of 17% during this period (Fig. 3). During the same period, the Willapa Bay plants that had been herbivore-free over the summer increased in biomass by an average of 1% (not significantly different from the San Francisco Bay plants), while the Willapa Bay plants that had been exposed to herbivory during the summer lost an average of 65% of their biomass, even though the herbivores had been removed (Fig. 3).

After two seasons of herbivore exposure, none of the San Francisco Bay plants in either of the treatments had died (Table 2). Among the Willapa Bay plants, a single plant in the no-herbivory treatment died, while 11 plants (37%) in the herbivory treatment died (Table 2). There was variation in mortality rate among the Willapa Bay herbivory clones, with one clone suffering 100% mortality and another 0% mortality (Table 2).

The response of Maryland plants to herbivores was similar to that of the San Francisco Bay plants, with plants exposed to herbivory attaining similar biomass to herbivore-free plants (Figs. 1 and 2). The replicates of the Willapa Bay founder clone were only exposed to 8 weeks of herbivory, and after that period of exposure,

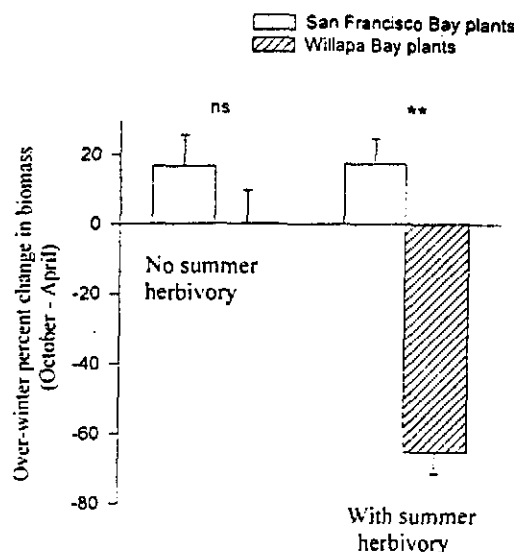


Fig. 3 Over-winter percent change in biomass for Willapa Bay and San Francisco Bay plants. All treatments were free of plant-hoppers over the winter. Willapa Bay summer herbivory plants lost biomass over winter, while San Francisco Bay summer herbivory plants gained biomass (**significant difference between populations, $P < 0.001$, ns no significant difference between populations, $P > 0.05$). Error bars represent 1 SE. We also tested whether the difference in proportional change in biomass between the no-herbivory and herbivory treatments differed between populations. The difference in change in biomass was significantly greater for the Willapa Bay population, indicating a significantly stronger effect of herbivory on the over winter growth of the Willapa Bay plants (t -test on clone means, $t = 3.05$, Bonferroni-corrected $P = 0.03$).

Table 2 Mortality of smooth cordgrass after two seasons of greenhouse growth in herbivore-exposed plants and herbivore-free controls

	Mortality (% of clonal replicates)	
	Herbivory	No herbivory
San Francisco Bay	0	0
Willapa Bay	37	3
Willapa Bay - by clone		
Diam5	0	0
Palix8	17	17
Lead2	17	0
Diam10	50	0
Oyst2	100	0

the herbivory plants averaged 85% of the biomass of herbivore-free plants. A linear extrapolation for the effect of 22 weeks of herbivory (as experienced by the other Willapa Bay plants during the first year) gives an estimated response of the Willapa Bay founder clone herbivory plants having only 58% of the biomass of herbivore-free plants, which is a stronger response to herbivory than observed among the San Francisco Bay plants (Fig. 1). This estimate of the Willapa founder clone's response to herbivory may be conservative because the detrimental effects of herbivory on growth are probably compounded over time to some degree, rather than simply linear.

Growth of herbivore-free control plants

By the end of the two seasons of greenhouse growth, the herbivore-free Willapa Bay plants had increased in biomass by 7.2 times on average, while the San Francisco Bay herbivore-free plants had increased in biomass by an average of 24 times. This overall difference in means between populations was significant (t -test, $t=6.13$, $P<0.01$); however, there was also overlap between the Willapa Bay and San Francisco Bay clones in net herbivore-free growth. For example, San Francisco Bay clone coy81 and Willapa Bay clone lead2 both averaged a 13-fold increase in biomass after two seasons of growth. The Willapa Bay clone that suffered 100% mortality in the herbivory treatments did not grow less in the absence of herbivory than other Willapa Bay clones (Tukey test after ANOVA, $P>0.56$ for all comparisons). In fact, two other Willapa Bay clones (diam10 and palix8) averaged smaller increases in biomass when not exposed to herbivores.

Planthopper choice experiments

Following the introduction of 7 planthoppers to each plant in May, the planthoppers multiplied over the summer to densities exceeding 100 per plant by September (Fig. 4). Planthoppers were observed to move freely and frequently between leaves of Willapa Bay and San Francisco Bay plants. There were no significant differences in number of planthoppers on San Francisco Bay versus Willapa Bay plants during the first 66 days of the initial experiment, however by days 95 and 108, the Willapa Bay plants had attracted significantly more planthoppers than the San Francisco Bay plants (univariate F -tests, $P<0.05$). On the final census (day 122), the Willapa Bay plants continued to average more planthoppers than San Francisco Bay plants, but this difference was not significant at the $P=0.05$ level ($F_{1,8}=3.70$, $P=0.09$). For the plants exposed to planthoppers beginning in August, there was a similar trend of initially similar numbers of planthopper on both San Francisco Bay and Willapa Bay, followed by higher average numbers of planthoppers on Willapa Bay plants after 28 days (Table 3), but these differences were not statistically significant for any census period (univariate F -tests, $P>0.26$).

At day 95, the percentage of leaves with 50% or more dead (brown) tissue on the Willapa Bay plants averaged 64% and was significantly greater than San Francisco Bay plants, which only averaged 28% of leaves with 50% or more dead tissue (paired t -test, $t=6.5$, $P<0.001$). The difference in the proportion of dead or dying leaves was a record of *Prokelisia* damage up to around day 85, since tissue does not completely brown until 7–10 days after feeding (C. C. Daehler, unpublished work). The greater damage to Willapa Bay plants was therefore observed before differences in planthopper densities between San Francisco Bay and Willapa Bay plants had developed, suggesting the Willapa Bay plants are less toler-

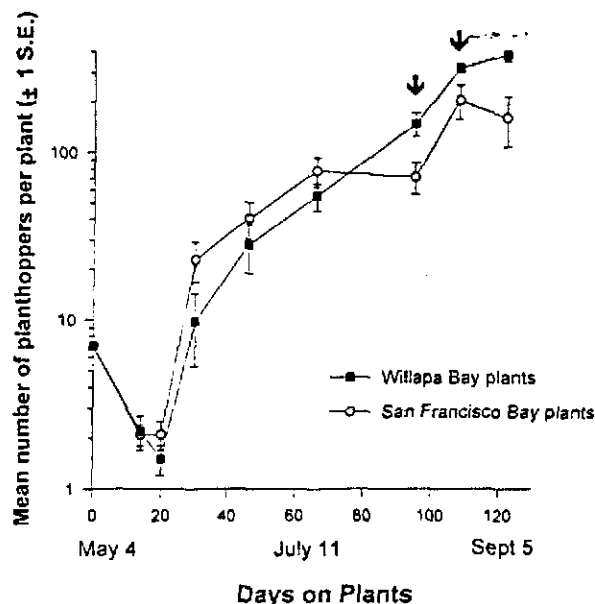


Fig. 4 Comparison of mean number of planthoppers on Willapa Bay and San Francisco Bay plants over time, when inoculated in May. Arrows indicate significant differences between populations. There were no significant differences between populations until after day 94 when Willapa Bay plants had significantly higher planthopper loads than San Francisco Bay plants

Table 3 Planthopper counts on smooth cordgrass when planthoppers were given a choice between plants from San Francisco Bay and Willapa Bay, beginning in August

Days of exposure	Average number of planthoppers per plant	
	San Francisco Bay	Willapa Bay
6	38±15	37±12
13	79±23	77±25
28	162±40	213±32
43	117±24	143±20

ant of planthopper herbivory, in addition to being preferred by the planthoppers over time.

Nitrogen analyses

Throughout the summer, the greenest leaves among the Willapa Bay plants were a darker green than the greenest leaves on San Francisco Bay plants, suggesting higher leaf nitrogen content in Willapa Bay plants (Munsell 1977 color reference 7.5 GY 4/2 to 4/4 for Willapa Bay versus 7.5 GY 4/6 to 5/6 for San Francisco Bay). The nitrogen analyses showed that planthopper herbivory did not affect total green leaf nitrogen content, however total leaf nitrogen content did differ significantly between the San Francisco Bay and the Willapa Bay plants (Table 4). The Willapa Bay clones averaged 70% more nitrogen in their leaf tissues than San Francisco Bay clones. The Maryland plants were similar to the San Francisco Bay plants in nitrogen content, while the Willapa Bay foun-

Table 4 Comparison of average percent nitrogen content in green leaf tissue for smooth cordgrass plants from San Francisco Bay, Willapa Bay and Maryland in herbivore-exposed and no-herbivory

	Origin of plants			
	San Francisco Bay	Willapa Bay founder	Willapa Bay	Maryland
Herbivory	0.884±0.056 ^a	1.656±0.092 ^b	1.437±0.015 ^b	0.947±0.027 ^a
No Herbivory	0.946±0.048 ^a	1.432±0.056 ^b	1.304±0.160 ^b	0.993±0.090 ^a

treatments (±1 SE). Values with different *superscripts* are significantly different (Bonferroni-corrected linear contrasts, $P < 0.05$)

der clone was similar to other Willapa Bay clones in nitrogen content (Table 4). Although leaf nitrogen measurements were made only in September, the consistent color difference between the Willapa Bay and San Francisco Bay plants suggested that they differed in nitrogen content throughout the summer.

Discussion

Herbivore resistance refers to any genetically controlled quality that results in one population (or other unit of interest) being less damaged by a particular herbivore than another (Kennedy and Barbour 1992). Based on above-ground biomass measurements from five clones, the Willapa Bay, Washington population was less resistant to herbivory than the San Francisco Bay and Maryland populations. Below-ground biomass measurements were not made in this study because of difficulty separating roots from vermiculite; however, in previous studies of herbivory on smooth cordgrass, above-ground biomass was strongly correlated with below-ground biomass ($r=0.95$, Daehler and Strong 1995). In an earlier trial herbivory experiment, shoot-root ratios for 4-month-old seedlings averaged near 1 for both Willapa Bay and San Francisco Bay plants (C. C. Daehler, unpublished work). General observations of root and rhizome growth in the present study gave no indication of a difference in shoot-root ratios between the two populations (C. C. Daehler, personal observation). The higher sensitivity of the Willapa Bay population to herbivory could be the result of a founder effect, genetic drift, natural selection in Willapa Bay, or any combination of these factors.

Evidence for a founder effect

The sensitivity of the putative Willapa Bay founder clone to short-term herbivory suggested that the difference in resistance between the Willapa Bay and San Francisco Bay populations may in part be due to a founder effect. The difference in total leaf nitrogen between the Willapa founder clone and San Francisco and Maryland plants also suggests a founder effect, since all other Willapa Bay clones tested shared the higher leaf nitrogen content of the founder clone. The Willapa Bay founder clone and other Willapa Bay clones also differed from the San Francisco Bay and Maryland plants in that they generally

produced smaller leaves, but more numerous shoots (C. C. Daehler, unpublished work). Sayce (1988) reported "dense-type" growth among seedlings and older smooth cordgrass plants in the field in Willapa Bay. These "dense-type" plants were similar in morphology to our greenhouse-grown Willapa Bay plants, suggesting that the growth characteristics observed in the greenhouse may be common in the field. Under common growing conditions, clones of smooth cordgrass collected at various sites along the Atlantic coast of North America vary greatly in growth characteristics like stem density and size (Anonymous 1992), indicating that geographic differences between the original source populations of smooth cordgrass in Willapa Bay and San Francisco Bay may be one cause of differences between these populations.

Evidence for further loss of resistance to herbivory by drift or selection

High variation in resistance to herbivory among the Willapa Bay clones suggests that some plants in Willapa Bay have lower resistance to planthopper herbivory than others as a result of either drift or selection. In particular, clone oyst10 suffered 100% mortality under planthopper herbivory, indicating an extremely low herbivore resistance relative to other clones tested and relative to the Willapa Bay founder clone. This especially low resistance to herbivory was not due to an intrinsically slower growth rate relative to other Willapa Bay clones, nor could the lower resistance be attributed to unusually high leaf nitrogen content (oyst10 averaged 1.56% nitrogen, compared to the overall average of 1.43% for all Willapa Bay clones). The geographic location of the oyst10 maternal plant at Oysterville, relatively close to the site of the founder clone (approximately 14 km across the bay) compared to the other sites from which plants were tested, does not provide evidence for a cline of decreasing resistance to herbivory with increasing distance from the founder clone. Oyst10 would not be predicted to survive in a habitat where *P. marginata* is present, and the finding of a clone with such a low level of resistance in the Willapa Bay population suggests that some plants in Willapa Bay now have lower herbivore resistance than the founder.

Possible causes of differences in resistance

Many sap-feeding insects are known to transmit viral diseases to their host plants (Racch and Irwin 1988; Nault and Ammar 1989), and one possibility is that the Willapa Bay plants were highly susceptible to an unknown debilitating virus transmitted by *Prokelisia*, resulting in apparently low resistance to herbivory among Willapa Bay plants. We find this hypothesis unlikely since planthoppers were occasionally found on the no-herbivory plants and they would probably have inoculated the no-herbivory Willapa Bay plants with the virus as well. The herbivore-free Willapa Bay plants appeared healthy in all respects.

Kennedy and Barbour (1992) list four plant strategies for reducing damage by herbivores: (1) association with other species; (2) escape in time or space; (3) tolerance; or (4) physical or chemical defenses, including resistance due to non-preference herbivores. In the case of smooth cordgrass, which generally grows in monospecific stands, the differential response to herbivory between the two populations probably involves a combination of differences in planthopper preference and differences in plant tolerance to herbivory.

The Willapa Bay plants were preferred by the planthoppers over San Francisco Bay plants after an initial period of planthopper colonization. This delayed preference was probably not due to seasonal changes in the plants because when fresh plants were added to the experiment in mid-summer, preference again required several weeks to develop. The planthoppers may have been attracted to the higher nitrogen content of Willapa Bay plant leaves, and this high nitrogen content may have become more apparent to the planthoppers either following a period of sampling different plants (Sogawa 1982) or following some initial plant damage that increased free amino acid concentrations in the leaf tissue (Bacheller 1990). In a New Jersey saltmarsh, Denno et al. (1980) found the highest densities of *P. marginata* on leaves that had the highest crude protein content. Crude protein is correlated with total leaf nitrogen (Denno 1983), suggesting that the planthoppers prefer leaf tissue with high nitrogen. *Prokelisia* densities were also higher in those smooth cordgrass stands having higher overall levels of crude protein (Denno et al. 1980), and in experimentally fertilized smooth cordgrass plots (Vince et al. 1981; Stiling et al. 1991), suggesting that the planthoppers are attracted to high-nitrogen stands. Other planthopper species are similarly attracted to higher nitrogen plants in the field (Kushwaha and Chand 1988). These observations suggest the *Prokelisia* planthoppers prefer leaf tissue that is higher in nitrogen, and this is a likely reason for the planthopper preference for Willapa Bay plants observed in this study.

Herbivore preference is probably not the sole cause of differences in resistance between the populations because a higher proportion of dead or dying leaves were observed on Willapa Bay plants even before differences in the number of planthoppers between Willapa Bay and

San Francisco Bay plants had developed. The differences in morphology between plants of the Willapa Bay and San Francisco Bay populations may also have contributed to differences in planthopper tolerance. The shorter, thinner stems and leaves, on average, of the Willapa Bay plants probably allowed a relatively greater proportion of the plant's tissue to be physically accessible by the planthoppers' short feeding stylets.

Blossey and Notzöld (1995) hypothesized that if resources are limited and resistance to herbivory is costly, then introduced plant populations growing in the absence of herbivory may evolve increased allocation to biomass at the expense of allocation to resistance to specialized herbivores. In contrast, we found that plants with faster growth rates had higher resistance to herbivory. Even within populations, the correlation between plant resistance and plant performance without planthoppers was positive ($r=0.65$ and $r=0.95$ for the San Francisco and Willapa Bay populations, respectively). In a comparison of two populations of the grass *Agropyron smithii* differing in grazing history, plants from the historically defoliated population grew faster and may have been better able to capture resources and store them below-ground (Polley and Detling 1988). Slower overall growth of the herbivore-free Willapa Bay plants compared to the herbivore-free San Francisco Bay plants could have led to decreased herbivore tolerance in the Willapa Bay plants, since plants with more rapid growth may often be more tolerant to herbivory (Rosenthal and Kotanen 1994).

The "trade-offs" approach to predicting the relationship between resistance and growth rate (Blossey and Notzöld 1995) does not consider effects of inbreeding (Charlesworth and Charlesworth 1987; Husband and Schemske 1996), which could act to reduce the average biomass of plants in introduced populations, especially if populations are established from a single introduction of a few founders. Inbreeding depression is likely to be an important factor affecting plant growth rates in introduced populations of smooth cordgrass since inbred (selfed) progeny have 30–90% slower growth rates than outbred progeny (Daehler 1996). Extreme inbreeding in the Willapa Bay population would have been unavoidable given that the population was founded from a single clone, and the slower growth of Willapa Bay plants in the absence of herbivory could be due to greater effects of inbreeding in that population, relative to the more recently introduced San Francisco Bay plants. Inbred individuals of *Impatiens palida* had slower growth rates than outcrossed individuals and also suffered greater mortality under herbivory (McCall et al. 1994). If inbreeding depression is responsible for slower growth in the Willapa Bay plants, then the founder (presumably outcrossed) should be more vigorous than the average inbred progeny now established in Willapa Bay. Unfortunately this test has very low power using the data from this experiment, and a larger experiment would be needed to provide conclusive evidence of more rapid growth in the Willapa Bay founder. An alternative explanation for the observed population growth rate differences

could be that the Willapa Bay plants were less well adapted than San Francisco Bay plants to our greenhouse growing conditions, despite our maintenance of greenhouse temperatures within the normal range experienced by the plants in southern Washington.

Implications for biocontrol

Current efforts to control established smooth cordgrass in Willapa Bay involve herbicides or cutting, and the effectiveness of these expensive methods over large areas is questionable (Aberle 1993). Previous field studies of the effects of *P. marginata* herbivory on smooth cordgrass in San Francisco Bay indicated that the planthopper would be unlikely to limit the spread of smooth cordgrass there due to its minor impact on the plants (Daehler and Strong 1995). However, the low resistance of the Willapa Bay population to herbivory by *P. marginata*, as observed in this greenhouse study, suggests biocontrol of smooth cordgrass in Willapa Bay may be an option worth exploring in Washington State.

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STATUS, PREDICTION AND PREVENTION OF INTRODUCED CORDGRASS *Spartina* spp. INVASIONS IN PACIFIC ESTUARIES, USA

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Abstract

Along the Pacific coast of North America, four introduced cordgrass species (*Spartina alterniflora*, *S. anglica*, *S. patens* and *S. densiflora*) have thus far invaded five isolated estuaries. Dense growth of introduced *Spartina* spp. reduces open mud feeding habitats of shorebirds, while in the upper intertidal, introduced *Spartina* spp. compete with native salt marsh vegetation. Prediction of *Spartina* invasions is facilitated by the remarkable restriction of these species to distinct estuarine habitats which generally lack interspecific competitors and herbivores. We used physical characteristics to identify 31 specific sites along the US Pacific coast that are vulnerable to future *Spartina* invasions and then used species characteristics, like native latitudinal range and past invasion success, to predict which *Spartina* species will be likely to invade these sites in the future. All 31 sites were predicted to be vulnerable to *S. alterniflora*, while the other invasive *Spartina* spp. may be restricted to a subset of the vulnerable sites. At a finer scale, within a vulnerable site, the mean tidal range can be used to predict the extent of spatial spread of a *Spartina* sp. after colonization. These prediction techniques might be used to identify and prioritize sites for protection against future invasions. We suggest that a cost-effective way to prevent the transformation of unique North American Pacific mudflat and saltmarsh communities into introduced *Spartina*-dominated marshes is to survey the vulnerable sites frequently and eliminate introduced *Spartina* spp. propagules before they spread. Copyright © 1996 Published by Elsevier Science Limited

Keywords: *Spartina*, cordgrass, invasion, Pacific, prediction.

INTRODUCTION

Cordgrasses *Spartina* spp. often dominate intertidal mudflats of estuaries on the Atlantic and Gulf coasts of

the Americas where they can form vast monospecific stands. On the Pacific coast of North America, however, *Spartina* spp. are usually conspicuously absent from estuaries, leaving the mid- and lower-intertidal of most mudflats devoid of vegetation. Only *Spartina foliosa* is native to the Pacific coast of North America, and the growth range of this species is restricted to the upper intertidal fringes of California's estuaries.

Several species of *Spartina* not native to the Pacific coast of North America are known to be highly invasive as demonstrated by their successful introductions around the world (e.g. Ranwell, 1967). In this paper, we summarize the status and distribution of introduced *Spartina* spp. in Pacific estuaries and describe some effects of these invasions. We then illustrate how vulnerable invasion sites and the extent of spatial spread within sites may be predictable for *Spartina* spp. The remarkable restriction of *Spartina* spp. to distinctive habitats, the variability among *Spartina* spp. in environmental tolerances, and the lack of established plant communities at most invasion sites greatly facilitate prediction. Finally, we suggest how the predictability of *Spartina* spp. invasions might be effectively used as a management tool.

THE GENUS *Spartina* – ORIGIN AND CHARACTERISTICS

Biogeographic patterns suggest that the genus *Spartina* originated on the Atlantic and Gulf Coasts of North America (Chapman, 1977). Mobberley (1956) recognized 14 species of *Spartina*, of these 13 are native to the Americas, while *S. maritima* is thought to be native to Europe. All species of *Spartina* are perennial and salt-tolerant; most grow in coastal areas or along stream banks, although one species, *S. spartinae*, can be found on terrestrial high ground (Table 1) (Mobberley, 1956). *Spartina townsendii* and *S. anglica*, differing in ploidy level, both originated within the last 150 years through hybridization between *S. maritima* and introduced *S. alterniflora* in Britain (Raybould *et al.*, 1991). The high chromosome numbers in all species of

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Table 1. Some characteristics of the genus *Spartina*. Summarized from Mobberley (1956) unless noted

Species	Chromosome number	Known to be invasive	Habitat	Native to
<i>S. alterniflora</i>	62 ^a	+	Intertidal	North America Atlantic/Gulf
<i>S. maritima</i>	60	+	Intertidal	Europe
<i>S. townsendii</i>	62	+	Intertidal	Britian
<i>S. anglica</i>	120, 122, 124 ^b	+	Intertidal	Britian
<i>S. patens</i>	28, 35, 42	+	Upper intertidal	North America Atlantic/Gulf
<i>S. densiflora</i>	60 ^c	+	Upper intertidal	South America Southern
<i>S. foliosa</i>	60 ^d		Intertidal	North America Pacific
<i>S. pectinata</i>	42, 70, 84	+/-	Brackish, terrestrial	North America Central Interior, Atlantic
<i>S. cynosuroides</i>	28, 42		Brackish	North America Atlantic/Gulf
<i>S. bakeri</i>	42		Brackish and FW lakes	North America Florida/Georgia
<i>S. gracilis</i>	42		Alkaline lakes stream banks	North America Central Interior
<i>S. spartinae</i>	28		Beach, terrestrial	North America Gulf/Central America

^a Marchant (1970).^b Marchant (1968).^c Spicher & Josselyn (1985).^d Parnell (1977).

Spartina suggest polyploid origin of the extant species. Several species may vary intraspecifically in ploidy level (Table 1). Seven of 14 species recognized by Mobberley (1956) are known to be invasive as defined by successful spread following introduction to a new continent (Table 1).

PHYSICAL EFFECTS ON ESTUARIES

Spartina spp. can accrete and hold sediment in intertidal areas that they invade. The rigid, densely packed stems decrease the rate of tidal flow, causing suspended sediment to precipitate, while dense root mats trap sediment. Randerson (1979) has suggested that the root mat is the primary cause of sediment accumulation. In New Zealand, rates of sediment accumulation in both *S. alterniflora* and *S. townsendii* have been reported at around 4 cm/year, while adjacent open mud showed no change (Bascand, 1970). Similar rates of sediment accumulation have been reported for *S. anglica* in England (Ranwell, 1964, 1967). In the Netherlands, a sediment

accumulation of 1.8 m over 22 years has been attributed to colonization of mudflats by *S. anglica* (Ranwell, 1967). Growth of *Spartina* spp. along river banks and tidal channels can restrict water flow and cause widening of the floodplain (Asher, 1991). Introduced plants that modify their physical environment in distinct ways, like through altering substrate characteristics, often have great ecological effects on native communities (Daehler & Strong, 1994).

IMPACT OF INTRODUCED *Spartina* ON NATIVE COMMUNITIES

The ecological impacts of *Spartina* invasions have been documented primarily through observational studies. Introduced *Spartina* spp. are often inferred to outcompete native salt marsh plants in the intertidal zone (Scholten & Rozema, 1990; Frenkel, 1991; Callaway & Josselyn, 1992). In Britain's lower intertidal, *S. anglica* has invaded the eel grass *Zostera* zone (Corkhill, 1984), reducing food available to certain herbivorous wildfowl

(Way, 1991). In the clayey upper intertidal in Britain and the Netherlands, *S. anglica* outcompetes native *Puccinellia*, confining the native to a narrow intertidal zone of only a few decimeters (Scholten & Rozema, 1990). *S. patens* introduced to Oregon invades the native *Deschampsia caespitosa*-*Scirpus maritimus* community, forming monospecific stands (Frenkel & Boss, 1988; Frenkel, 1991). In San Francisco Bay, *S. alterniflora* grows both higher and lower in the intertidal than *S. foliosa* and invades established stands of this native (Callaway & Josselyn, 1992). In Humboldt Bay, CA, introduced *S. densiflora* produces large quantities of wrack that can smother native *Salicornia* and *Distichlis*. The resulting bare areas may then be colonized by monospecific stands of *S. densiflora* (P. Kittelson, pers. comm.).

Introduced *Spartina* spp. have clear negative effects on some native plant species, but an associated negative effect on invertebrate communities is less obvious and little studied. While there are some indications that Dungeness crab *Cancer magister* populations may be negatively affected by *S. alterniflora*'s invasion of Willapa Bay, WA (Sayce, 1991), densities of benthic invertebrates may be greater beneath introduced *Spartina* spp. than in adjacent open mud (Way, 1991; Josselyn *et al.*, 1993; P. Kittelson, pers. comm.). Dumbauld *et al.* (1994) found hardshell clams *Tapes philippinarum* to be more abundant inside the perimeter of *S. alterniflora* clones invading Willapa Bay, WA, compared to adjacent open mud, although towards the centers of clones, hardshell clams were less abundant. Softshell clam *Mya arenaria* abundance was not affected by *S. alterniflora* (Dumbauld *et al.*, 1994). In perhaps the most detailed study to date, mud beneath *S. alterniflora* plants in Brazil was found to contain more species and higher densities of invertebrates than adjacent open mud; however, overall species abundances were less even beneath *S. alterniflora* and the abundance of suspension feeders was negatively correlated with the presence of *Spartina* (Lana & Guiss, 1991). *Spartina* spp. may increase the number and diversity of invertebrates by increasing the habitat's structural complexity. At the same time, invertebrates beneath *Spartina* spp. may be less vulnerable to predation by shorebirds. In California, no consistent differences were found in the invertebrate communities beneath introduced *S. alterniflora* and native *S. foliosa* (Josselyn *et al.*, 1993), suggesting that the introduced species will not greatly alter the invertebrate community structure as native stands of *S. foliosa* become invaded by *S. alterniflora*.

A major ecological concern associated with the worldwide invasion of intertidal open mud by introduced *Spartina* spp. has been that shorebird populations will be negatively affected through a loss of feeding grounds (Hubbard & Partridge, 1981; Way, 1991; Callaway & Josselyn, 1992). While *S. alterniflora*'s invasion of established *S. foliosa* stands in San Francisco Bay will be unlikely to affect shorebird

feeding, its invasion of open mud in the mid-intertidal will affect the availability of open-mud shorebird feeding areas there. Goss-Custard and Moser (1988) found that the spread of *S. anglica* was related to decreases in populations of dunlin *Calidris alpina* in certain estuaries in Britain. Shorebirds generally do not forage in *Spartina* stands (Lee & Partridge, 1983; Millard & Evans, 1984; Davis & Moss, 1984; Josselyn *et al.*, 1993) so areas invaded by introduced *Spartina* spp. are effectively lost feeding grounds to shorebirds.

VULNERABILITY OF PACIFIC ESTUARIES TO INVASION

Pacific estuaries are geologically very young. The major Pacific estuaries are 'drowned' river valleys that formed with the global sea level rise at the end of the last ice age, less than 10,000 years ago (Atwater *et al.*, 1979). Several Pacific marshes are only a few hundred years old (Macdonald & Barbour, 1974). *Spartina foliosa* is the only species of *Spartina* native to the Pacific coast with a range extending only from Baja California north to Bodega Bay, California (Mobberley, 1956; Spicher & Josselyn, 1985). The species is morphologically and cytologically very similar to *S. alterniflora* native to the Atlantic and Gulf coasts of North America (Table 1) but its tolerance of tidal submersion is much less than its Atlantic relative (Callaway & Josselyn, 1992). *S. foliosa* may be a sister species to *S. alterniflora* that evolved following the formation of the land bridge between North and South America some six million years ago.

The estuaries along the Pacific coast are essentially islands. Most are separated by hundreds of km of high-energy wave-swept coast. These 'island' communities may be species-poor owing to their recent creation. The absence of *S. foliosa* from a few estuarine habitats in California that have been created in the last 100 years may be due to poor long-distance dispersal. Geographic isolation may also have been the major factor that kept Pacific estuaries free of other *Spartina* species until the last 150 years of human-facilitated dispersal.

STATUS OF *Spartina* INVASIONS IN PACIFIC ESTUARIES

Four species of introduced *Spartina* are currently invading Pacific estuaries. The sites of invasion range from San Francisco Bay north to British Columbia. *Spartina alterniflora* is invading San Francisco Bay, CA, Suislaw Estuary, OR, Willapa Bay, WA, and Puget Sound, WA. The invasion is proceeding most rapidly in Willapa and San Francisco Bays. During the 4-year period from 1988 to 1992, *S. alterniflora* in Willapa Bay invaded 800 ha of open mud to cover a total of 1000 ha. In San Francisco Bay, *S. alterniflora* spread from about 650 circular patches in 1990 (Callaway & Josselyn, 1992) to more than 1000 circular patches in 1993,

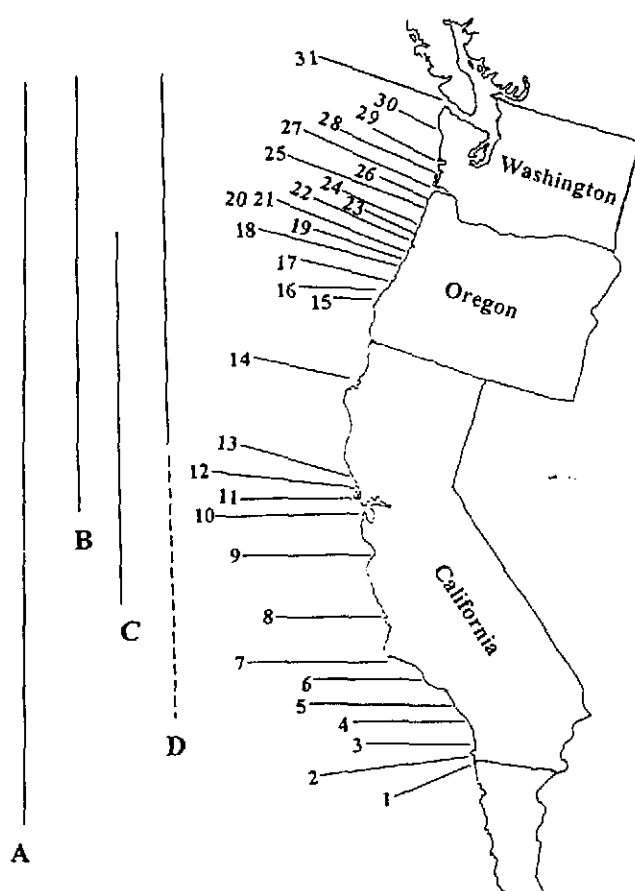


Fig. 1. Sites along the Pacific coast of the United States that are vulnerable to invasion by introduced *Spartina* species and the predicted range of invasion for different *Spartina* species. A, *S. alterniflora*; B, *S. anglica*; C, *S. densiflora*; D, *S. patens*. Sites in bold italic print have already been invaded by one or more introduced *Spartina* spp. *1, Tijuana River Estuary, CA; *2, San Diego Bay, CA; *3, Mission Bay, CA; 4, Santa Margarita River, CA; *5, Anaheim Bay / Newport Bay, CA; *6, Mugu Lagoon, CA; 7, Carpinteria Marsh, CA; 8, Morro Bay, CA; *9, Elkhorn Slough, CA; *10, San Francisco Bay, CA; *11, Drake's Estero, CA; *12, Tomales Bay, CA; *13, Bodega Harbor, CA; 14, Humboldt Bay, CA; 15, Coquille Bay, OR; 16, Coos Bay, OR; 17, Umpqua Bay, OR; 18, Suislaw Estuary, OR; 19, Alsea Estuary, OR; 20, Yaquina Bay, OR; 21, Siletz Bay, OR; 22, Nestucca Bay, OR; 23, Sand Lake, OR; 24, Netarts Bay, OR; 25, Tillamook Bay, OR; 26, Nehalem Bay, OR; 27, Columbia River, OR/WA; 28, Willapa Bay, WA; 29, Gray's Harbor, WA; 30, Hoh River Estuary, WA; 31, Puget Sound, WA.

*. Native *S. foliosa* is present.

plus several areas of continuous monoculture (C.C.D., pers. obs.). *S. alterniflora* also began to invade Humboldt Bay, CA. A small patch was discovered in the early 1980s which spread to occupy approximately 1000 m² by 1989. At that time, a control program was initiated and the patch was eradicated over a 3-year period by smothering with a plastic sheet and sand bags (K. Kovacs, pers. comm.).

Spartina anglica is invading Puget Sound, WA. In 1977 transplants were brought from Puget Sound to San Francisco Bay (likely, as part of a saltmarsh

restoration project) where they now occupy less than 1 ha (Spicher & Josselyn, 1985). *Spartina patens* is invading Cox Island and Suislaw Estuary, OR and Puget Sound, WA. The Oregon population is spreading rapidly (Frenkel, 1991); however, the Puget Sound population has been the focus of an intensive eradication effort and all known plants are currently covered with sheets of black plastic (J. Civile, pers. comm.). San Francisco Bay has some *S. patens* at one site in the north bay, but it doesn't appear to be spreading (Spicher & Josselyn, 1985). *Spartina densiflora* has invaded Humboldt Bay, CA and was transplanted to San Francisco Bay where it is now spreading (Spicher, 1984).

PREDICTING FUTURE INVASION SITES

The Pacific coast of North America is depauperate of estuaries compared to the Atlantic and Gulf Coasts (Schubel & Hirschberg, 1978). Furthermore, not all estuaries and lagoons on the Pacific coast are likely to be invaded by *Spartina* spp. To identify potential sites of *Spartina* spp. invasion we employed two criteria. First, the presence of the native *S. foliosa* was used as an indicator of areas susceptible to invasion by other *Spartina* spp. (e.g. Daehler & Strong, 1993). Second, we considered areas to be susceptible to *Spartina* spp. invasion if they were protected from wave action but exposed to tidal action year round. No *Spartina* sp. has been found to persist in areas subject to consistent wave action (Mobberley, 1956) and wave energy has been negatively correlated with survival in both *S. alterniflora* and *S. anglica* (Hardaway *et al.*, 1984; Gray, 1992). Continuous tidal action, on the other hand, is certainly not a prerequisite for growth, as evidenced by vigorous growth in greenhouses. However, in surveys for *Spartina* spp., the invasive species of the genus are conspicuously absent, even within their native ranges, from all sites that are seasonally closed to tidal action or with very little tidal activity (e.g. Christiansen & Moller, 1983; Onuf, 1987). Absence of tidal action can result in anoxic waters, increased salinity, and a buildup of sulfides in the substrate that can kill *Spartina* spp., perhaps by preventing nitrogen uptake (Morris, 1980; Bradley & Dunn, 1989). Tidal action may also be necessary to wash away senescent leaves and stems that otherwise can inhibit spring growth (C.C.D., pers. obs.). Using these criteria, we identified sites along the Pacific coast that are predicted to be vulnerable to *Spartina* invasion (Fig. 1). A total of 31 sites were identified along the Pacific coast of the United States. At most of these sites no *Spartina* sp. is yet present.

WHICH SPECIES WILL INVADE?

Having identified sites vulnerable to invasion by *Spartina* spp., we used the native climatic and latitudi-

nal ranges of these species to predict which *Spartina* spp. would be most likely to invade the identified sites along the Pacific coast (Fig. 1). Information collected on successful and failed invasions of *Spartina* spp. around the world (e.g. Ranwell, 1967; Aberle, 1990) suggested that the latitude and climate of the site where a *Spartina* sp. is introduced can serve as a good predictor of invasion success.

Comparing previous invasions of *S. alterniflora* and *S. anglica* following introductions around the world reveal differing successes of the two species in relation to latitude of the introduction site. *S. anglica* has done better than *S. alterniflora* at higher latitudes, rapidly spreading and outcompeting *S. alterniflora* when present in Britain, France, Netherlands, and Northern China (Ranwell, 1967), while *S. anglica* invasions often fail at lower latitudes like Brazil, South Africa, the North Island of New Zealand and Louisiana, USA (Ranwell, 1967; Bascand, 1970; Aberle, 1990; M. Rejmanek, pers. comm.). The fact that *S. anglica* did successfully invade parts of the South Island of New Zealand, where the climate is notably cooler than the North Island (Lee & Partridge, 1983; Aberle, 1990), suggests that *S. anglica* requires a cool-temperate climate for successful spread, rather than strictly a high latitude.

Recognizing the slow spread of *S. anglica* in San Francisco Bay, we defined this area as the likely southern limit of invasion by *S. anglica*. *S. townsendii* is very similar to *S. anglica* in ecological tolerance but, due to the sterility imposed by its hybrid origin, it spreads only by rhizomes. *S. alterniflora* ranges natively on the Atlantic coast from Florida to Canada, so all estuaries susceptible to *Spartina* invasion on the Pacific coast were expected to be vulnerable to invasion by *S. alterniflora*. The native range of *S. patens* on the Atlantic coast also extends from Canada to Florida; however, this species is far more abundant north of Maryland where it can be found in vast monocultures above the *S. alterniflora* intertidal zone (Merrill, 1902;

Adam, 1990). Large monocultures of *S. patens* also naturally occur within the Mississippi delta of Louisiana at latitudes comparable to Southern California; however, these *S. patens* stands are limited to brackish waters, generally with a salinity no greater than 15‰ (J. B. Grace, pers. comm.). In southern California, such brackish water habitats are very rare due to arid summers with virtually no precipitation. The unsuccessful spread of *S. patens* introduced to San Francisco Bay (Spicher & Josselyn, 1985; D.R.S., pers. obs.) but the rapid spread of *S. patens* northward in Oregon (Frenkel, 1991) suggests that San Francisco Bay is near the southern limit of vigorous *S. patens* spread, although this is tentative and limited colonizations might occur further south.

S. densiflora is native to southern South America (Mobberley, 1956). The conspicuous absence of *S. densiflora* in central and northern Brazil suggests that it does poorly in warmer latitudes, while its absence from the southernmost points of South America suggests that it requires a cool-moderate climate for growth. *S. densiflora* is presently successfully spreading in San Francisco and Humboldt Bays (Spicher & Josselyn, 1985), suggesting that it may be capable of invading estuaries further south. These differential climatic and latitudinal tolerances were used to make predictions about which species of *Spartina* would be likely to invade different sites along the Pacific coast of the United States (Fig. 1).

PREDICTION AT A FINER SPATIAL SCALE: HOW MUCH AREA WILL BE INVADED?

Once a species has begun invading an area we can ask how spatially extensive the invasion will eventually become. This can be predicted for several invasive species of *Spartina* using known intertidal growth ranges. For example, the growth range (in vertical meters) of *S. alterniflora* at sites ranging from Florida to Massachusetts is positively correlated with mean tidal range (in vertical meters) (Fig. 2, $r^2 = 0.91$, $p < 0.01$) (McKee & Patrick, 1988; see also Hardaway *et al.*, 1984). A similar correlation has been determined for *S. anglica* (Gray, 1992). Knowing the mean tidal range at an invasion site and taking advantage of these linear correlations, it is a simple matter to estimate the growth range of a specified *Spartina* sp. in the intertidal (Fig. 3). To check the validity of the correlation for Pacific estuaries, we calculated the mean tidal range in San Francisco Bay and then evaluated the vertical growth range of *S. alterniflora* at the San Bruno invasion site in San Francisco Bay. The mean tidal range was calculated from 1994 tide tables to be 1.26 m. Using the regression from McKee & Patrick (1988), the predicted growth range of *S. alterniflora* was 1.1 vertical meters within the intertidal. The established *S. alterniflora* at San Bruno had a growth range of only 0.82 vertical meters in 1990 (Callaway & Josselyn, 1992); however,

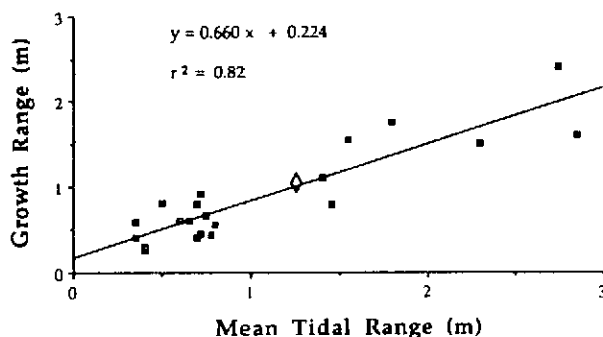


Fig. 2. The relationship between mean tidal range (vertical m) and growth range of *Spartina alterniflora* (vertical m) along the Atlantic coast of North America (redrawn with permission from McKee & Patrick, 1988). The diamond indicates the mean tidal range and actual growth range of introduced *S. alterniflora* in San Francisco Bay (San Bruno invasion site).

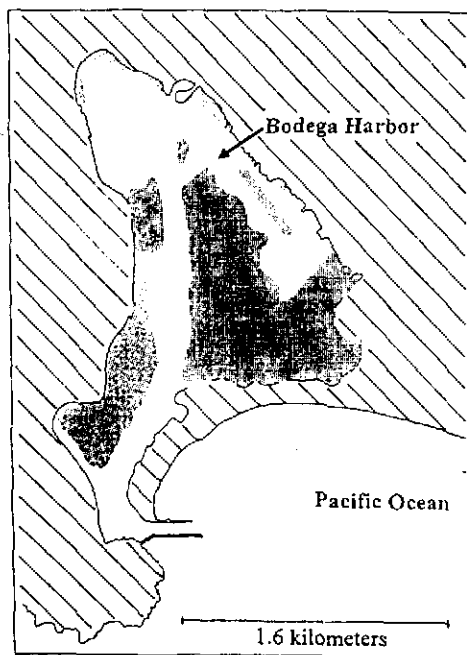


Fig. 3. Predicted spatial distribution of *S. alterniflora* in Bodega Harbor should the species be introduced there. Extent of spatial spread was predicted using the correlation between growth range and mean tidal range (see text).

the invasion is in its early stages and experimental transplants along a tidal gradient there indicate that *S. alterniflora* will eventually have a growth range between 1.1 and 1.2 vertical meters (Daehler & Strong, unpubl. data). This data point sits close to the regression (Fig. 2), suggesting that predictions of the spatial extent of invasion on the Pacific coast can indeed be made based on the correlation with mean tidal range. Furthermore, the upper limit of *S. alterniflora* in the intertidal can also be predicted from mean tidal range (McKee & Patrick, 1988). With the ability to predict the upper growth limit and the growth range in vertical meters, it then becomes possible to predict the specific areas within a site that are likely to be invaded.

As an example, we have calculated the area of Bodega Harbor predicted to be invaded by *S. alterniflora* if the species were introduced there (Fig. 3). The mean tidal range at Bodega Harbor is about 1.22 m (calculated from tide charts) so the predicted mean growth range is about 1 m (McKee & Patrick, 1988) while the upper growth range of *S. alterniflora* is predicted to be about 0.6 m above the midpoint between mean high and mean low water (McKee & Patrick, 1988). Using a US Geological Survey (USGS) topographic map, we predicted that about 175 ha (about 65% of the harbor) would be invaded by *S. alterniflora* if the species were introduced there. A similar prediction of the area that would be invaded by *S. anglica* could be made from the predictive relationship given by Gray (1992). *Spartina patens* also occurs over predictable tidal ranges within its native (e.g. Bertness &

Ellison, 1987; Adam, 1990) and non-native (Frenkel & Boss, 1988) habitat range, and transplant studies have measured its environmental range in the absence of competition (Bertness, 1991). *S. densiflora* has been less studied; however, its maximal tidal growth range has been experimentally measured in San Francisco Bay (Spicher, 1984) and these data could be used to predict the maximum area potentially invadable by *S. densiflora*. These predictions can be used to give an indication of the physical and ecological modification that could take place at specific sites should a specific *Spartina* sp. be introduced, making it possible to prioritize areas to be protected against *Spartina* invasion. This simple method of prediction does not take into account changes in hydrology that may take place in an area as the *Spartina* invasion progresses and sediments accumulate, so this method may underestimate the eventual spatial extent of spread. On the other hand, within the growing *Spartina* marsh, deeply dissected tidal channels that lack *Spartina* are also likely to form, decreasing to some extent the total area of *Spartina* coverage.

MANAGEMENT OF PACIFIC ESTUARIES VULNERABLE TO *Spartina* INVASION

We know that many Pacific estuaries are vulnerable to *Spartina* spp. invasions and we can make predictions about which species will invade and where. A major issue is how much human resources should be expended in an effort to eliminate present invasions and prevent future invasion. The possibility of biological control is interesting, but would require an expensive long-term commitment that, to date, has not been given serious considerations by agencies that would have to foot the bill. Cordgrasses have many species of insect and nematode herbivores (Strong *et al.*, 1984). If introduced without their natural enemies, these herbivores might control introduced *Spartina* spp. An alternative method of control currently being explored in Willapa and San Francisco Bays is the voluminous application of herbicides to reduce *S. alterniflora* coverage (Aberle, 1990; K. Sayce, pers. comm.; S. Jones, pers. comm.). This method of control is also uncertain and requires long-term planning and financing.

The costs of allowing *Spartina* invasions to proceed are even more uncertain and difficult to evaluate. Introduced *Spartina* spp. can rapidly alter the character of Pacific estuaries, transforming expanses of open intertidal mud into vast monocultures of dense grass. The major threat to conservation seems to lie in the reduction of open-mud feeding areas for wading and shorebirds. Along the Pacific flyway, estuaries are few and far between, and starvation due to reduced shorebird feeding areas might lead to a decline in populations of many migratory birds. At Bodega Harbor, 77 bird species seasonally forage in intertidal and subtidal areas (Standing *et al.*, 1975). As predicted in Fig. 3,

invasion of Bodega Harbor by *S. alterniflora* would result in the loss of most of these foraging areas.

Spartina invasions also have negative effects on traditional human uses of Pacific estuaries. Areas suitable for oyster culture at Willapa Bay have been reduced by *S. alterniflora*'s spread there (Sayce, 1988). *Spartina*'s rapid accretion of sediment can clog navigation and flood control channels which can be expensive to dredge. But there may be some valuable aspects of introduced *Spartina* spp. in Pacific estuaries.

At least one bird species may benefit from *Spartina* spp. invasions in Pacific estuaries. Endangered California clapper rails *Rallus longirostris* build their nests in *S. alterniflora* (E. Harding-Smith, pers. comm.) and the presence of nesting clapper rails has been correlated with vigorous *Spartina* growth (Foin & Brenchley-Jackson, 1991). Gun clubs, which have been a source of intentional *Spartina* spp. introductions, have long known that *Spartina* stands can attract certain duck species. *Spartina* spp. can also increase estuarine net primary productivity, as *Spartina* marsh communities have amongst the highest levels of net primary productivity known (Lieth & Whittaker, 1975; Gallagher *et al.*, 1980). Some of this productivity is exported through tidal flow as senescent leaves are washed away, while *in situ* decomposing rack generated from senescent culms can support a large and diverse community of nematodes (Alkemade *et al.*, 1993) and larval invertebrates (C.C.D., pers. obs.). Some benthic invertebrate species thrive beneath stands of *Spartina* spp., in comparison with open mud (Lana & Guiss, 1991).

Despite these possible positive aspects of *Spartina* invasions, a major reason to restrict introduced *Spartina* spp. from Pacific estuaries is a growing realization of the ecological uniqueness of native Pacific estuarine communities. Plant communities in Pacific salt marshes are known to differ greatly with latitude (Macdonald, 1977), but ecological relationships between Pacific salt-marsh species have rarely been studied as they have on the Atlantic coast. The importance and value of unique communities has been widely discussed (Wilson, 1988). The expense of maintaining native communities free of dominating exotic species will surely increase in the future. With *Spartina* spp. invasions, a simple but very effective strategy is to identify introduced propagules early through surveying (by air or by shore) the vulnerable sites. Identified propagules can then be eliminated prior to spread at minimal cost. This strategy was successful in eliminating *S. alterniflora* from Humboldt Bay, CA (K. Kovacs, pers. comm.) and will probably succeed with *S. patens* in Puget Sound (J. Civile, pers. comm.). Whether invasions that have significantly progressed, like those of *S. alterniflora* in Willapa and San Francisco Bays, can be eradicated is still unknown, but given past experience (Aberle, 1990), the answer may be no. Although prospects for eradicating all introduced *Spartina* spp. from the Pacific coast are not encouraging, at least

there remain some 25 Pacific estuaries in the United States that are free of introduced *Spartina*. With appropriate precautions and minimal expense we have a good chance of protecting them from future invasion.

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Impact of High Herbivore Densities on Introduced Smooth Cordgrass, *Spartina alterniflora*, Invading San Francisco Bay, California

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ABSTRACT: *Spartina alterniflora*, smooth cordgrass, invading San Francisco Bay, California (USA), is attacked by high densities of a plant hopper, *Prokelisia marginata*, and a mirid bug, *Trigonotylus uhleri*. Both herbivores are sap-feeders. We investigated the impact of these herbivores on *S. alterniflora*'s growth rate, vegetative spread, and seed production by manipulating herbivore densities in the field and in a greenhouse. Herbivore densities in the field peaked in early fall, with *P. marginata* averaging more than 300 individuals per mature culm of *S. alterniflora* (about 100,000 per m²) and *T. uhleri* densities exceeding 10 per culm (about 3,000 per m²). Field reductions of herbivore densities by approximately 70% with insecticidal soap did not result in greater vegetative growth rates or lateral spread of plants; plants grew vigorously with the highest densities of insects. In the greenhouse study, conducted with seedlings, herbivory significantly reduced plant mass and tiller number in some but not all replicate herbivory treatments. In both field and greenhouse, there were significant differences between some clones' growth rates independent of herbivory. Inflorescence production in the field was not affected by reduced-herbivory treatments. Seed set was low under conditions of both natural and reduced herbivory, averaging 0.4%. Despite densities of *P. marginata* and *T. uhleri* that are much higher than typically observed in areas where *S. alterniflora* is native, herbivory by these particular insects appears to have little impact and is unlikely to limit *S. alterniflora*'s spread through San Francisco Bay.

Introduction

Spartina alterniflora Loisel., a perennial salt marsh grass native to the Atlantic Coast of North America, has been introduced to estuaries around the world (Ranwell 1967; Aberle 1990; Mumford et al. 1990). Some introductions have been intentional (to stabilize shoreline erosion), while others have been accidental such as through the unloading of ship's ballast (Aberle 1990). *Spartina alterniflora* was introduced to San Francisco Bay, California in the mid-1970s during a marsh restoration project (Spicher and Josselyn 1985; Daehler and Strong 1994), but the plant is now widely recognized as an imposing invader. *Spartina alterniflora* threatens to transform the bay's open mud flats into vast monocultures of dense, 2 m-tall grass, modifying invertebrate communities and resulting in great loss of shorebird feeding areas (Callaway and Josselyn 1992). Attempts to control *Spartina* invasions around the

world by mechanical disruption, shading, and herbicides have been costly and usually unsuccessful (Aberle 1990; Mumford et al. 1990). Very little is known about the impact of insect herbivores on cordgrass marshes (Adam 1990). The work of Bertness et al. (1987) and Bertness and Shumway (1992) suggests that insect herbivores may have great impact on *S. alterniflora*'s sexual reproduction in its native Rhode Island habitat; however, the potential for biological control of introduced *S. alterniflora* by insect herbivores has yet to be explored. Biological control may have advantages over traditional control methods for *S. alterniflora* in terms of labor, monetary cost, and human health hazards (DeBach and Rosen 1991).

In San Francisco Bay, *S. alterniflora* is attacked by high densities of two sap-feeding insect herbivores. In this study we use field manipulations and greenhouse experiments to assess the impact of herbivory on the vegetative growth and seed production of introduced *S. alterniflora* in San Francisco Bay. The results are used to evaluate the potential for these herbivores to control *S. alterniflora*'s invasion of San Francisco Bay.

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Materials and Methods

STUDY ORGANISMS

Spartina alterniflora, smooth cordgrass, typically grows in extensive monocultures in its native habitat, the intertidal mud flats of the Atlantic and Gulf coasts of North America (Adam 1990). The plant can spread by both seed and vegetative fragments and is presently abundant at several sites in south San Francisco Bay. In recently colonized areas, *S. alterniflora* grows in circular patches separated by open mud. These circular patches consist of individual genetic clones (Daehler and Strong 1994). The two insect herbivores attacking *S. alterniflora* in San Francisco Bay are *Prokelisia marginata* Van Duzee (Homoptera), a plant hopper, and *Trigonotylus uhleri* Reuter (Miridae), a mirid bug. Both insects are *Spartina* specialists and are common herbivores of *S. alterniflora* on the Atlantic Coast of North America (Denno 1977; Strong and Stiling 1983; Denno 1985). In San Francisco Bay, these herbivores also feed on the native *Spartina foliosa*. *P. marginata* appears to be a native herbivore of *S. foliosa* on the Pacific Coast of North America (Wilson 1982). During three summers of censusing (1991–1993), *Prokelisia marginata* reached peak densities approaching 1,000 individuals per culm of *S. alterniflora* and consistently reached densities of 300 per culm by early fall (Daehler unpublished data). These densities are far higher than densities typically reported from *S. alterniflora*'s native habitat (e.g., Denno et al. 1980; Strong and Stiling 1983). *Prokelisia marginata* completes three to four fairly discrete generations per season in San Francisco Bay, with increasing peak densities from June until November, when populations drop sharply until spring (Roderick 1987; Daehler unpublished data). *Trigonotylus uhleri* was not recorded to occur on the Pacific Coast of North America prior to our 1993 collection in San Francisco Bay (identified by T. J. Henry, Systematic Entomology Laboratory, United States Department of Agriculture). During the summer of 1993, *T. uhleri* reached densities as high as 10 individuals per mature culm of *S. alterniflora*.

FIELD MANIPULATION OF INSECT DENSITIES

To evaluate the influence of herbivory on plant growth and reproductive output, insect herbivores were killed on individual clones of *S. alterniflora* in the field using a contact insecticide, 1:50 Safer Insecticidal Soap (Safer Inc., Newton, Massachusetts, USA). We tested for effects of this insecticide on the growth of *S. alterniflora* (see Effects of insecticide on plants, below). A total of 16 circular clones were used to evaluate the effects of herbivory on

plant growth in the field. Clone sizes ranged from 1.5 m to 2.5 m in diameter, and each was separated from surrounding plants by 1–3 m of open mud. Half of the clones were randomly assigned to be sprayed with insecticide followed by a freshwater rinse. The remaining eight control clones were sprayed with only a freshwater rinse. Spraying was done weekly for 14 wk, beginning in early July and ending in mid October. During a 3-wk period beginning in late August, spraying was done twice per week, since a large cohort of winged adult *P. marginata* recolonized sprayed patches more rapidly during that time. To measure the effectiveness of insecticide spraying, herbivore densities were estimated on control and insecticide-sprayed plots on several dates, both just prior to spraying and mid-week after spraying. Densities were estimated by counting all herbivores on five different stems of a clone. Counted stems were chosen randomly with the constraints that stems were approximately average height for the clone and could be counted without trampling the clone. Counts from at least four different control and sprayed clones were used to estimate herbivore densities during each census. This procedure proved to be very time consuming, especially on control clones, so counts could not be made every week.

EFFECT OF INSECTICIDE ON PLANTS

Initial greenhouse trials had shown that long-term, repeated spraying of *S. alterniflora* with Safer Insecticidal Soap could cause etiolation of leaves under the following conditions: spraying during strong sunlight and high leaf temperature (above about 28°C, also not advised by the manufacturer); allowing residue to build up on leaves as a result of repeated spraying and drying. We took several steps to ensure a minimum effect of the insecticide on our field plants. To avoid strong sunlight and high leaf temperatures, we usually sprayed within 1 h of sunrise, and never more than 3 h past sunrise. After spraying with insecticide, we rinsed clones with fresh water to eliminate build-up of residue. Tides normally flooded the clones twice daily, removing any remaining residues from most leaves and washing away residue from the mud beneath clones.

We conducted experiments to test the effect of a similar treatment regime on greenhouse plant growth. In the first experiment, a total of 40 potted *S. alterniflora* seedlings of approximately uniform size were used. Half were randomly assigned to be sprayed weekly with insecticide followed by a freshwater rinse. The controls were rinsed with fresh water only. These plants were fertilized biweekly with a solution of Plantex 20-20-20 fertilizer. In the second experiment, seeds were germinated from

10 different clones from the field site and a pair of similar-size seedlings was chosen from each maternal clone. One seedling from each pair was randomly assigned to be sprayed with insecticide while the other was sprayed with water. These plants were fertilized twice per week with the same fertilizer solution as the first experiment. The experiments were carried out for 10 consecutive weeks, and during the last 3 wk plants were sprayed twice per week. At the end of the experiment, plants were harvested, dried to a constant mass at 70°C, and compared between treatments.

VEGETATIVE GROWTH RATES IN THE FIELD

Prior to the first spraying in early July, five mid-sized stems (about 30 cm tall, hereafter referred to as juvenile stems) and 10 small shoots (about 15 cm tall, hereafter referred to as shoots) were marked on each clone using numbered flags. The height of each of these stems was measured weekly during the course of the experiment. Stem height is strongly correlated with dry mass of stems in *S. alterniflora* (Nixon and Oviatt 1973). Using stems collected from our study site, a logarithmic transformation of both height and dry mass yielded a correlation of $r = 0.983$ ($n = 51$, $p < 0.001$).

To compare vegetative growth rates between sprayed and control clones, we used a discrete measure (McGraw and Garbutt 1990) of relative growth rate (RGR),

$$RGR = (h_t - h_{t-1})/h_{t-1}$$

where h_t is the height at time t and h_{t-1} is the height 1 wk later (e.g., Thomas and Bazzaz 1993). Because height is strongly correlated with biomass, this measure of growth is directly proportional to growth rate measured by change in biomass (Dachler unpublished results).

LATERAL SPREAD IN THE FIELD

In early July, a 3-m-long wire was pressed in the mud as a tight semicircle around the edge of each circular clone. At that time, no shoots were outside the wire. The wire was held firmly in place with several stakes. In mid-October, we counted the number of new shoots outside the wire to quantify lateral spread.

SEXUAL REPRODUCTION IN THE FIELD

At the conclusion of the field experiment in early November, all inflorescences from the 16 experimental clones were harvested just prior to natural loosening of the spikelets. The relative number of inflorescences (per m²) were determined as a measure of allocation to flowering. All spikelets were then counted and the proportion of spikelets con-

taining seed was used as a measure of seed production.

GREENHOUSE HERBIVORY EXPERIMENT

In mid July, *S. alterniflora* seedlings were potted with a mixture of 25% Bodega Bay mud and 75% Vermiculite (by volume) into 4 cm diameter × 15 cm deep growth tubes and placed into four trays. Each tray contained a total of 30 plants, with five individuals from each of six different maternal families. The position of each individual within a tray was randomized and plants were generously spaced to minimize edge effects. Three trays of plants were then inoculated with *P. marginata* and *T. uhleri* collected from the field (initial densities: approximately 5 *P. marginata* per plant and approximately 0.25 *T. uhleri* per plant). Insects were observed to move readily between plants within inoculated trays by hopping; insect densities were determined from biweekly counts. The fourth tray of 30 plants served as a herbivore-free control. Plants were grown on the same greenhouse bench and the position of trays was rotated biweekly to minimize lighting effects. To prevent colonization of the control plants by herbivores, the control tray was always separated from the infested plants by a 1.5 m-wide barrier of dead, dried *S. alterniflora* stems. This barrier was approximately the same height as the initial experimental plants and was highly effective. The occasional insect observed on control plants was immediately removed by hand. Biweekly, each tray was given 1 g of Plantex 20-20-20 fertilizer dissolved in water; growth tubes were kept saturated with fresh water. After 12 wk of herbivory, plant shoots and roots were dried to a constant mass at 70°C. Dry mass and number of shoots per plant were compared between herbivore treatment and control plants.

STATISTICS

Statistical analyses were performed using the SYSTAT system (Wilkinson 1990). Differences in growth rate between insecticide-treated and control clones in the field were tested using ANOVA with clone nested within treatment (insecticide versus control). Growth rates were treated as repeated measures (Sokal and Rohlf 1981; Neter et al. 1990). Treatment means were then compared for each measurement time using univariate F-tests corrected for multiple comparisons by a sequentially rejective Bonferroni procedure (Holm 1979). Separate ANOVAs were used for the measurements of juvenile stems and measurements of shoots, since the timing of growth was not directly comparable (juvenile stems reached maximum height much earlier than shoots). Growth rate measurements toward the end of the season could not be

TABLE 1. Effect of insecticide treatment on the growth of greenhouse *Spartina alterniflora* plants. Measurements were made on plant dry mass (g) and are given as ± 1 standard deviation.

	Insecticide	Control	p-value
Biweekly Fertilizer Addition			
Aboveground biomass	0.321 \pm 0.078	0.341 \pm 0.072	0.418 ^a
Total plant biomass	0.772 \pm 0.154	0.873 \pm 0.234	0.115 ^a
Twice-weekly Fertilizer Addition			
Aboveground biomass	7.88 \pm 5.84	8.61 \pm 5.19	0.563 ^b
Total plant biomass	10.74 \pm 7.60	12.32 \pm 7.34	0.351 ^b

^a Independent samples t-test between insecticide-sprayed and control (water sprayed) plants, $n = 40$.

^b Paired samples t-test between pairs of sibling seedlings of the same initial size, one sibling sprayed with insecticide, the other sprayed with water, $n = 20$.

analyzed using the ANOVA because many zeros in the data violated the assumption of normality (although heteroscedasticity was not a problem). For these end-of-season measurements we used the nonparametric Mann-Whitney U statistic to compare mean growth rates of insecticide-treated and control clones (Daniel 1990). Lateral growth rate and relative number of inflorescences were compared between sprayed and control clones using t-tests assuming separate variances (Wilkinson 1990). The greenhouse herbivory experiment was analyzed with ANOVA using initial plant height as a covariate. Tray and family were treated as main effects. We then tested for significant differences among the trays using a Tukey test for multiple comparisons (Neter et al. 1990).

Results

EFFECT OF INSECTICIDE ON GREENHOUSE PLANTS

For both greenhouse experiments, there were no significant differences between the insecticide-sprayed and control greenhouse plants in either aboveground plant biomass or total plant biomass (Table 1, t-tests), indicating that our spray treatments do not significantly affect the growth of *S. alterniflora*.

IMPACT OF INSECTICIDE ON HERBIVORE DENSITIES

Virtually all herbivores counted on insecticide-treated patches were immigrants from surrounding plants, since the insecticide proved extremely effective in killing insects at the time of spraying. Mid-week censuses showed that sprayed clones averaged herbivore densities that were 10–30% of controls. A full week after spraying, herbivore densities on insecticide-treated clones usually averaged less than 50% of those on control clones (Figs. 1

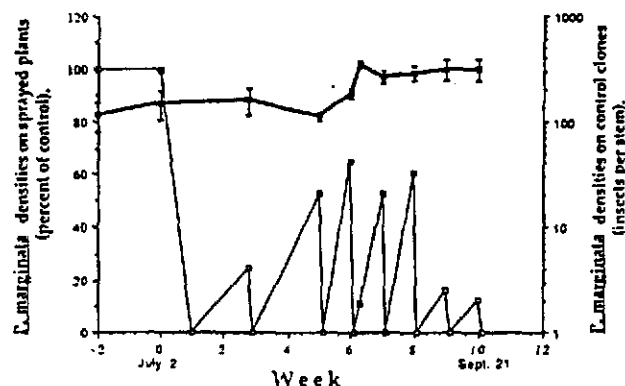


Fig. 1. Mean number of *Prokelisia marginata* per stem on control *Spartina alterniflora* plants during the course of the herbivore reduction experiment (thick line, right axis, log scale, error bars indicate 1 SE) and mean *P. marginata* densities on insecticide-treated plants, expressed as percent of control plants (left axis, thin line). Dates of insecticide treatment are indicated by zero *P. marginata* densities on the left axis. Insecticide-treated clones usually carried far less than half of the herbivore load of control clones. Insect censuses were terminated after September 21 (week 10); however, insecticide treatments continued through October (week 14).

and 2). Throughout the experiment, the range of mean *P. marginata* densities on insecticide-treated plants a full week after insecticide treatment was 40–177 insects per stem, while control clones averaged 113–853 insects per stem.

EFFECTS OF HERBIVORY-FIELD STUDY

For growth measurements on juvenile stems, there was a significant difference between insecticide-treated and control clones only during the first week following spraying, with insecticide-treated clones having a more rapid growth rate (Fig.

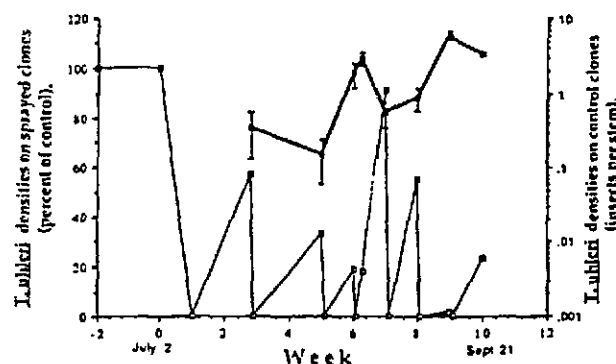


Fig. 2. Mean number of *Trigonotylus uhleri* per stem on control *Spartina alterniflora* plants during the course of the herbivore reduction experiment (thick line, right axis, log scale, error bars indicate 1 SE) and mean *T. uhleri* densities on insecticide-treated plants, expressed as percent of control plants (left axis, thin line). Censuses of *T. uhleri* were not begun until week 3 and were terminated after week 10. Insecticide treatments were continued through October (week 14).

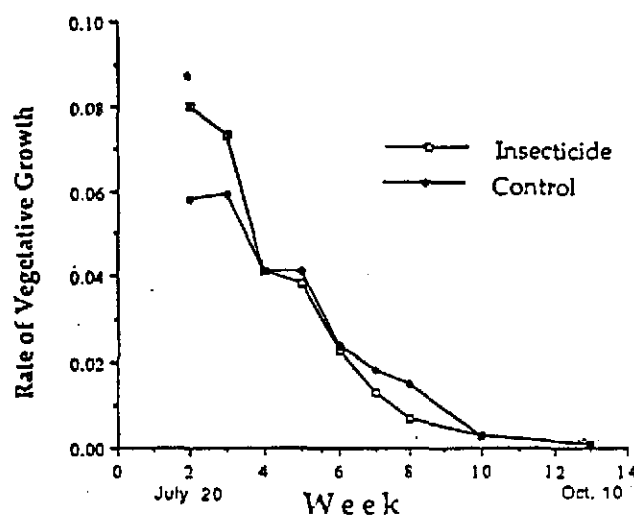


Fig. 3. Field vegetative growth rates ($\text{g g}^{-1} \text{wk}^{-1}$) measured from juvenile (initially about 30 cm tall) stems of *Spartina alterniflora* followed over summer on insecticide-treated (open squares) and control clones (solid diamonds). Asterisk indicates significant difference between insecticide-treated clones and controls (only on week 2). (Bonferroni test for multiple comparisons, $p < 0.05$). Growth rate declined through the summer and averaged near zero by week 10. Discrete growth rate was measured as $(\text{height at week } x + 1 - \text{height at week } x) / (\text{height at week } x)$. This measure is strongly correlated with growth rates measured from dry mass.

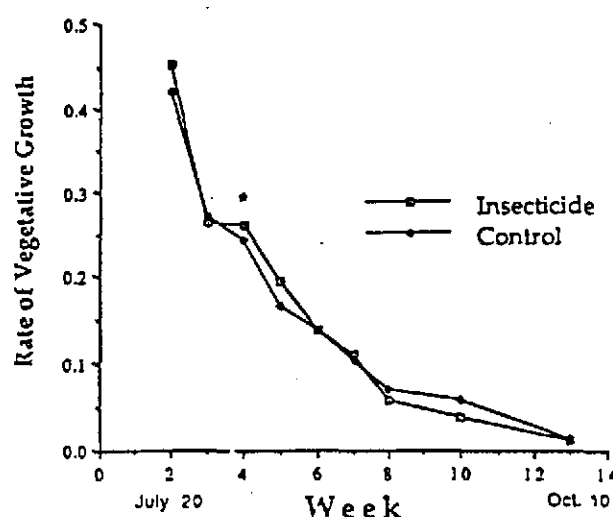


Fig. 4. Field vegetative growth rates ($\text{g g}^{-1} \text{wk}^{-1}$) measured from shoots (initially about 15 cm tall) of *Spartina alterniflora* followed over summer on insecticide-treated (open squares) and control clones (solid diamonds). Scale differs from Fig. 3. Asterisks indicate significant differences between insecticide-treated clones and controls (only on week 4) (Bonferroni test for multiple comparisons, $p < 0.05$). Growth rates approached zero by week 13. Discrete growth rate was measured as $(\text{height at week } x + 1 - \text{height at week } x) / (\text{height at week } x)$. This measure is strongly correlated with growth rates measured from dry mass.

3). For growth measurements on shoots, there was a significant difference only after the second week of measurements, with shoots from insecticide-treated clones growing more rapidly (Fig. 4). Both juvenile stems and shoots showed a significant effect of time, decreasing in growth rate through the season; however, shoots also showed a significant interaction of time and clone ($p = 0.004$), suggesting that different clones showed different patterns of growth over time. There was no treatment \times time interaction ($p = 0.441$). Insecticide-treated and control clones produced a similar number of inflorescences and both had equally low rates of seed set (Table 2). The rate of lateral spread was found to be positively correlated with clone area. This correlation was effectively removed by dividing the number of new shoots outside the marking wire by clone area. Using this relative measure, there was no difference between mean rate of spread of insecticide-treated and control clones (Table 2).

EFFECTS OF HERBIVORY, A GREENHOUSE STUDY

One week following inoculation of greenhouse plants, *P. marginata* densities averaged about 4 per plant (approximately 9 g^{-1} aboveground dry mass, compared to approximate field densities at the

time of 15 g^{-1} plant dry mass). By week 6, greenhouse densities had increased to levels similar to those in the field, and by week 10, following emergence of a large second cohort of eggs, greenhouse plants averaged $40 \text{ P. marginata g}^{-1}$ dry mass, while field plants only averaged $21 \text{ P. marginata g}^{-1}$ dry mass. Densities of *T. uhleri* on greenhouse plants were similar to field densities throughout the experiment, averaging about $1 \text{ T. uhleri g}^{-1}$ dry biomass.

In the greenhouse herbivore treatments, six out of 90 seedlings died, while none of the 30 control seedlings died. The seedlings that died were some of the smallest individuals at the start of the experiment (all less than 15 cm tall) and all dead

TABLE 2. Reproductive output and vegetative spread of *Spartina alterniflora* clones in the field with natural herbivory (control) and reduced herbivory (insecticide). p -values are given for t -tests assuming unequal variances. $n = 8$ clones per treatment.

	Insecticide	Control	p -value
Reproductive output			
Clones not flowering	1	1	
Inflorescences m^{-2}	8.2 ± 7.3	14.4 ± 13.6	0.28
Percent seedset	0.92 ± 0.18	0.44 ± 0.31	0.76
Vegetative spread			
New sprout m^{-1}	6.8 ± 3.4	10.7 ± 6.4	0.16

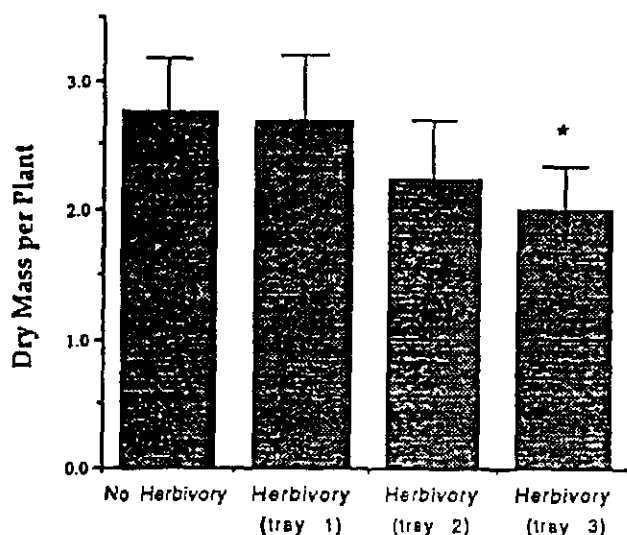


Fig. 5. Mean dry mass (g) of greenhouse plants without herbivory and greenhouse plants from three different trays subjected to herbivory by *Prokelisia marginata* and *Trigonotylus uhleri* for 12 wk. Error bars indicate 95% confidence intervals (Tukey HSD method) and the asterisks indicate a significant difference between herbivory and no herbivory plants ($p < 0.05$). Each replicate tray was inoculated with similar numbers of herbivores. Herbivore densities were similar to those observed in the field.

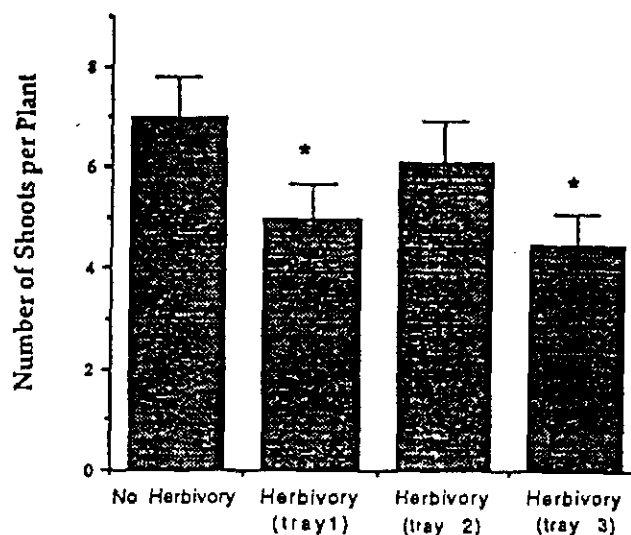


Fig. 6. Mean number of shoots on greenhouse plants without herbivory and greenhouse plants from three different trays subjected to herbivory by *Prokelisia marginata* and *Trigonotylus uhleri* for 12 wk. Error bars indicate 95% confidence intervals (Tukey HSD method) and the asterisks indicate a significant difference between herbivory and no herbivory plants ($p < 0.05$). Each replicate tray was inoculated with similar numbers of herbivores. Herbivore densities were similar to those observed in the field.

seedlings had grown less than 2 cm before dying. Dead plants were excluded from the statistical analyses.

Because aboveground biomass was found to be strongly correlated with total biomass ($r = 0.951$), an ANOVA was run only on total plant biomass, transformed logarithmically to fulfill assumptions of normality and homogeneity of variance. There was a significant overall effect of tray ($p = 0.033$); however, comparison of treatment means between the no-herbivory tray and herbivory trays shows that only one of the herbivore treatment trays had significantly lower mean plant biomass than the control tray (Fig. 5). There was also a significant family effect for total plant biomass ($p < 0.001$), but no interaction between family and treatment ($p = 0.33$).

In testing the effect of herbivory on total number of shoots, the data were log-transformed to fulfill the major assumptions of ANOVA. There was a significant effect of tray ($p = 0.043$). Examination of the means between the control tray and the herbivory trays showed that two herbivory trays averaged significantly fewer shoots than the control tray, but the third herbivory tray did not differ from the control (Fig. 6). There was a significant effect of family ($p = 0.001$) on shoot number and there was a significant family \times tray interaction ($p = 0.004$). This interaction became nonsignificant when one family that had shown an increase in

mean number of shoots in the herbivore treatment was excluded from the analysis.

Discussion

HERBIVORY AND VEGETATIVE GROWTH

Our manipulations of herbivore densities in the field suggest that the extraordinarily high *P. marginata* and *T. uhleri* densities have little consistent effect on vegetative growth rates of *S. alterniflora* in San Francisco Bay. The analyses based on shoots and juvenile stems had the power to detect approximately 12% and 20% differences, respectively, between mean growth rates of insecticide-treated and control plant during a given week of growth (at a family-wide significance level of 0.05). Greater differences in growth rates might have been observed in the field had we been able to exterminate continuously all herbivores on the insecticide-treatment clones; however, given the marginal differences observed in the greenhouse where control plants were virtually herbivore-free and environmental variance was minimized, we doubt if a large difference would have been found had all herbivores been exterminated in the field. The greenhouse study had the power to detect approximately a 25% difference in dry mass between herbivore and herbivore-free plants (at a significance level of 0.05).

Our study lasted for only one growing season

and there is a possibility that long-term, chronic herbivory by these sap-feeding insects may be slowing the vegetative spread of *S. alterniflora*. This hypothesis is not supported by a comparison of rates of lateral spread in San Francisco Bay, where plants suffer herbivory by *P. marginata* and *T. uhleri*, and in Willapa Bay, Washington, where no insect herbivores attack *S. alterniflora*. At both invasion sites the rates of lateral spread are similar, ranging from 0.5 m yr⁻¹ to 1 m yr⁻¹ (Sayce 1988; Daehler unpublished data).

In other studies of the effects of sap-feeding insects on plants, highly significant reductions in plant growth or survival have been observed, usually within 8 wk of the herbivore manipulations (e.g., Kantack and Dahms 1957; Mittler and Sylvester 1961; Mallott and Davy 1978; Kamm 1979; Wood et al. 1985; Reed and Semner 1992; Debernardinis et al. 1994). In most of these studies the plants were perennials, and the plants were always of agricultural importance. Not surprisingly, these studies document large effects of sap-feeders because the herbivores studied were recognized a priori as causing major economic losses in the crops.

On the other hand, in a noncrop plant (*Solidago altissima*), aphid feeding had no detectible effect on plant growth (Meyer 1993). More studies on sap-feeders of non-crop plants are needed to evaluate the range of impacts that sap-feeders might have on plant vegetative growth in nature. We suspect a bias toward reporting strong effects of herbivores on host plants. The large body of literature reporting major effects of sap-feeders on agricultural crops may not be relevant to natural systems given recent evidence suggesting wild plants may be more tolerant to herbivory than their domesticated crop relatives (Welter and Steggall 1993).

HERBIVORY AND PLANT MORTALITY

In the greenhouse study, herbivory did apparently kill a few of the smallest seedlings. The impact of herbivory on seedlings was expected to be higher than on established plants because seedlings lack the belowground reserves of adult clones (Harper 1977). On San Francisco Bay mud flats, we have never found evidence that insect herbivory alone causes death of seedlings, established clones, or even individual tillers. In the field, many seedlings grow alone on open mud and have virtually no herbivores. Interestingly, a potentially important cause of shoot mortality in the field is herbivory by rodents. Tracks and scats from unidentified rodents (either the muskrat, *Ondatra zibethica*, or black rat, *Rattus rattus*, both introduced) were often observed in the mud beneath *S. alterniflora* where young shoots had been freshly gnawed near

their bases. Attacks were patchy but thorough, with 20 or more young shoots being gnawed during single feeding bouts. During the course of the growing season, but primarily toward the end of the season, 19% of all our marked shoots were chewed near the base by rodents. These shoots always died (and were excluded from analysis after being chewed). But *S. alterniflora* is known to tolerate grazing and mowing, and in some cases, mowing plants as a control measure may even increase plant growth rate, stimulating the production of additional new shoots (Aberle 1990; M. Taylor personal communication). Van der Meijden et al. (1988) have suggested that a high root:shoot ratio may be an indication of ability to tolerate high herbivory, since these plants may have excellent regrowth capacity. The root:shoot ratio of *S. alterniflora* typically ranges from 1 to 2 (Smart 1986), comparable to that of *Senecio*, a plant cited as herbivory tolerant by van der Meijden et al. (1988).

HERBIVORY AND SEED PRODUCTION

Spartina alterniflora clones vary greatly in seed production in San Francisco Bay. Most clones set very few seeds (Daehler and Strong 1994). Reducing herbivory with insecticide treatments did not increase seed set in the present study. Previous work in *S. alterniflora*'s native range showed that herbivores damaged many ovules and anthers, causing reduced seed set (Berntness and Shumway 1992). The primary herbivore causing damage in that study was a grasshopper, *Conocephalus spartinae*, which is not present in San Francisco Bay. Sap-feeding insects have been shown to reduce seed set in some grasses, causing silvertop-white inflorescences with withered stems (Starks and Thurston 1962; Kamm 1979). Silvertop culms usually set no seed. We have never observed the symptoms of silvertop on *S. alterniflora*, although seed set is often very low independently of herbivory.

Other evidence that suggests sap-feeding insects in San Francisco Bay have very little effect on seed set comes from a comparative study of seed set in Willapa Bay, Washington (USA) (Daehler and Strong 1994). *Spartina alterniflora* introduced to Willapa Bay has spread in the absence of all insect herbivores, yet clones in Willapa Bay have a similar frequency distribution of seed set to those in San Francisco Bay, with most clones setting very few seeds. When seed set is low due to factors that may be intrinsic to the plant (like seed abortion), the relative effects of even heavy herbivory on seed set may be minor (e.g., Traveset 1994). Seed set in this primarily outcrossing invader may be limited by viable pollen, or abortion of fertilized or unfertilized ovules due to recessive lethal alleles (Weins et al. 1987) rather than herbivory.

POTENTIAL FOR HERBIVORE CONTROL OF *S. alterniflora*

The growth of the herbivore populations is seasonal and distinctly correlated with the above-ground growth of *S. alterniflora*. Sparse herbivore populations in May and June increase to very dense populations in September and October, which then drop rapidly during November (Roderick 1987; Daehler unpublished data). The population crash of herbivores in November is probably the result of mortality due to seasonal changes in plant nitrogen. Nitrogen content in all above-ground parts of *S. alterniflora* drops rapidly in late fall as mature stems die (Squiers and Good 1974). Seasonal changes in plant nitrogen occur independent of herbivory, and the accompanying herbivore population crashes suggesting this particular set of species in the *S. alterniflora* food web in San Francisco Bay is primarily donor-controlled (Strong 1992); the primary producer controls production of herbivores, carnivores, and detritivores, with consumers having little if any reciprocal effects upon levels of their resource species. The parasitoid *Anagrus delicatus* kills some eggs of *P. marginata*, but the mortality is low and inversely density-dependent (Stiling and Strong 1982; Strong 1989; Cronin and Strong 1990), so the top-down effects of natural enemies on *P. marginata* are minimal in San Francisco Bay.

One possible reason why high herbivore densities have so little effect on *S. alterniflora* is that the plant suffers no interspecific competition. It grows uncrowded, invading rich, open mud. Under these conditions, stresses due to light and nitrogen limitations are reduced in comparison with established stands. Herbivory can be most effective in damaging plants growing under stressed conditions like high plant density (Lee and Bazzaz 1980; Dirzo 1984). Often, herbivory can regulate a plant population indirectly by altering competitive hierarchies among plant species, making the attacked species more vulnerable to interspecific competition (Crawley 1983; Cottam et al. 1986; Louda et al. 1990). In the case of the monospecific *S. alterniflora* community of the lower intertidal, there are no plant competitive hierarchies for herbivores to alter, possibly making herbivore regulation of this plant especially difficult. In some cases, nitrogen supplements have been necessary for successful herbivore control of an introduced plant growing in monospecific stands (Thomas and Room 1986). In its native environment, *S. alterniflora* supplemented with nitrogen fertilizer did have higher herbivore densities; however, fertilized plants also had increased standing biomass (Vince et al.

1981), the opposite of what would be expected if herbivory were regulating plant biomass.

From both the field and greenhouse results of this study, it appears unlikely that herbivory by high densities of the sap-feeding insects *P. marginata* and *T. uhleri* alone will be able to control the invasion of *S. alterniflora* in San Francisco Bay. There is no evidence that feeding by these insects alone has an important effect on vegetative growth or seed production in the field. Other insects native to the Atlantic Coast of North America could act more effectively as biocontrol agents, especially if introduced without parasitoids. For example, insects with stem-boring larvae that kill meristems, like *Chilo plejadellus* (Lepidoptera), and inflorescence-killing midges like *Calamomyia alterniflorae* (Strong et al. 1984) would seem to have greater potential for controlling *S. alterniflora*; however, their introductions would require extensive, pre-release screening to ensure that no other plant species were attacked.

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Sierra Nevada Runoff into San Francisco Bay — Why Has It Come Earlier Recently?

Mike Dettinger, Dan Cayan, and Dave Peterson
USGS, San Diego

By the time most of the Sierra Nevada snowpack has melted each summer, freshwater outflows from the Sacramento-San Joaquin Delta to San Francisco Bay are typically small, even after the wettest winters. These small delta outflows during the warm months (in comparison with the large flows of winter and spring) are overwhelmed by salty coastal waters, and the bay becomes more and more salty as summer progresses. Because longer low-flow seasons allow the bay to become saltier, timing of the Sierra Nevada snowmelt and runoff, which are the source of the delta flows, has a profound influence on the salinity of the bay and, thus, can affect its ecosystems (Peterson *et al* 1995).

Consequently, a recent tendency toward earlier snowmelt and runoff — described in this article — is a matter of concern. Is it a symptom of global warming? Is it a response to local or regional urban heat-island effects? Or is it just a normal part of the variability of California's hydrology? These possibilities raise concerns also about how much earlier the low-flow seasons in San Francisco Bay might begin in the future if the observed trends continue

and how well the bay ecosystems will be able to cope with the flow-timing changes.

The "earlier runoff" trend was first noted by Maurice Roos, DWR, in 1987 (Roos 1987). Although it has much year-to-year variability, the runoff-timing trend can be detected by eye (Figure 1a) and is significantly different from random-chance occurrences according to a range of statistical tests (Dettinger and Cayan 1995). Since early in the century, the average April-June fraction of annual runoff has diminished from almost 50% to less than 40%. The trend toward smaller late-spring and early-summer fractions of each year's streamflow from the Sierra Nevada is shown in Figure 1a. This trend has been compensated for by a subtler set of opposite trends toward more winter and early-spring streamflow during the same period. The influence of these monthly trends on the overall timing of streamflow in the American River near Sacramento is shown in Figure 1b, in which the average recent flow regime is compared with the average flow regime from 30 years ago, when flows usually peaked almost a month later. Inspec-

tion of a large collection of streamflow records indicates that similar changes occurred throughout much of the western United States. A clue to their origin is that in the Sierra Nevada these changes are most accentuated in middle altitudes and are muted in streamflow records representing very high (more than 2,500 m) or very low (less than 1,000 m) altitudes.

The mechanism involved in these trends is mostly a hastening of the peak snowmelt period in recent decades in response to an observed trend toward warmer Januaries, Februaries, and Marches in the Sierra Nevada (Figure 2). Actually, this temperature influence is somewhat surprising, because historically the dominant control on seasonal runoff-timing fluctuations has been precipitation timing rather than temperature (Cayan *et al* 1993). Since the late 1940s, however, temperatures throughout the year in the Sierra Nevada have increased, with the January-March season experiencing the greatest warming, a total of about 2°F in 50 years (Dettinger and Cayan 1995). During the same period, precipitation timing has shown little if any overall

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Cordgrass Invasions Likely in Northern San Francisco Estuary

Donald R. Strong, University of California, Davis, Bodega Marine Laboratory

Open intertidal mud without vegetation is a hallmark of Pacific estuaries, in contrast to Atlantic and Gulf Coast estuaries where vast stands of monocots prevail. Smooth cordgrass, *Spartina alterniflora*, is the most aggressive of these intertidal plants; it is dense and tall, with thick, solid turfs of roots. Estuaries comprise a far smaller fraction of the Pacific than Atlantic and Gulf coasts of North America, and open mud without intertidal grasses is key to the ecology of the geologically young communities in low-energy intertidal environments of California, Oregon, and Washington. The openness of intertidal mud is crucial to shore birds, some marine mammals, fish, and invertebrates, as well as flood control, recreation, navigation, and the esthetics of our Pacific estuaries.

Smooth cordgrass has been inadvertently and purposefully introduced to several Pacific estuaries where it has spread, covered a large fraction of previously open mud, and caused great immediate economic harm to navigation and fish. The longer-term threats of these invasions include loss of precious foraging areas of shore birds and larval fish, as well as wholesale sediment accumulation and severe channelization. In San Francisco Bay,

smooth cordgrass has spread since the early 1970s from its introduction point to many sites in the south bay. Clogging the Alameda Flood Control Channel, it is now the object of an expensive and ecologically hazardous aerial herbicide spraying campaign. The longer-term threats to birds, fish, and water management are enormous. A special threat in the bay is to the noninvasive California cordgrass, *Spartina foliosa*, which remains high on the intertidal gradient and is the habitat of the California clapper rail and salt marsh harvest mouse, both endangered species. Smooth cordgrass overgrows California cordgrass and probably hybridizes with it.

North San Francisco Bay, San Pablo Bay, and Suisun Marsh are likely sites of invasion by smooth cordgrass. Salinity and tides in these areas are perfect for this alien. Fortunately, most seed produced by smooth cordgrass in the bay area is sterile, and spread here is mostly by clonal growth and fragmentation. Many clonal fragments break off in chunks of mud as large as an ice chest or larger. However, waves wash the mud away and leave the light-colored fibrous root masses to float or be carried to a new site. Most root masses are at least the

size of one's fist and are attached to a green stem with bilateral leaves. The stems and leaves can be up to a meter long in late summer, but even a small, stemless root mass can be a vigorous propagule. The most likely means of dispersal of root masses from the southern to the northern parts of the San Francisco estuary is inadvertent transport on dredges and other vessels, on boat trailers, or in bait or live seafood containers (smooth cordgrass was introduced to Willapa Bay, Washington, as oyster packing material).

The hopeful aspect of the likely smooth cordgrass colonization of the northern San Francisco estuary is that young, small colonies can be eradicated with the legal herbicide *Rodeo*, or even removed by hand. Young colonies are lime green, round patches of grass in the intertidal mud, usually close to mean high water. So far, all cordgrass that we know of in the northern parts of the San Francisco estuary is the native and valuable California cordgrass. Young colonies of the two species are difficult to distinguish, but any reddish coloration of upper roots or lower stems indicates the noxious alien, smooth cordgrass.

Interagency Program Technical Reports Since 1993

No.	Year	Title
34	1993	Proceedings of the Ninth Annual Pacific Climate (PACCLIM) Workshop K. Redmond, V. Tharp, editors
35	1993	Observations of the Early Life Stages of Delta Smelt, <i>Hypomesus transpacificus</i> , in the Sacramento-San Joaquin Estuary in 1991, with a Review of Its Ecological Status in 1988 to 1990 J. Wang, R. Brown
36	1994	Proceedings of the Tenth Annual Pacific Climate (PACCLIM) Workshop K. Redmond, V. Tharp, editors
37	1994	Delta Agricultural Diversion Evaluation 1992 Pilot Study S. Spaar
38	1994	Long-Term Trends in Benthos Abundance and Persistence in the Upper Sacramento-San Joaquin Estuary — Summary Report: 1980-1990 Z. Hymanson, D. Mayer, J. Steinbeck
39	1994	Seasonality and Quality of Eggs Produced by Female Striped Bass (<i>Morone saxatilis</i>) in the Sacramento and San Joaquin Rivers J. Arnold, T. Heyne
40	1995	Proceedings of the Eleventh Annual Pacific Climate (PACCLIM) Workshop C. Isaacs, V. Tharp, editors
41	1995	Food Habits of Several Abundant Zooplankton Species in the Sacramento-San Joaquin Estuary J. Orsi
42	In Review	Working Conceptual Model for the Food Web of the San Francisco Bay/Delta Estuary Estuarine Ecology Team
43	In Review	Observations of Early Life Stages of Splittail (<i>Pogonichthys macrolepidotus</i>) in the Sacramento-San Joaquin Estuary, 1988 to 1994 J. Wang

Newsletter

Autumn 1994

Readers are encouraged to submit brief articles or ideas for articles. Correspondence, including requests for changes in the mailing list, should be addressed to Randy Brown, California Department of Water Resources, 3251 S Street, Sacramento, CA 95816-7017.

Comments on a Peripheral Canal

H.K. Chadwick

My comments are in response to an article on a peripheral canal¹ published in the *Interagency Newsletter* a year ago.

First, my comments pertain to the concept of moving all CVP/SWP southern delta diversions to the Sacramento River rather than to a specific physical structure. Thus, my comments largely ignore important issues associated with the specific physical structure, which would affect the biological consequences substantially. This concept reflects my bias that if one builds a large conveyance facility to the Sacramento River, it is probably unwise biologically to continue diverting the relatively small remaining flows in the San Joaquin River.

I agree with the basic point in Wim's discussion that the well-being of some aquatic resources depends primarily on factors associated with outflow and that those resources would receive no benefit from a peripheral canal. Strong evidence suggests that longfin smelt,

starry flounder, and *Crangon franciscorum* are in this category. One wonders how many aquatic resources have such flow-dependent effects. A particular need is to explore evidence as to whether primary and secondary productivity in the lower estuary are related to flow.

In any event, certain resources in the estuary clearly depend on adequate outflow, regardless of the physical system used to divert water.

I also agree that a peripheral canal offers benefits only for species adversely affected by entrainment. Wim's description, however, might be interpreted as defining entrainment as only including organisms actually entering the CVP/SWP intakes. Entrainment must be defined to include any organisms diverted from natural migration paths or habitat by hydrodynamic changes caused by diversions or structures built to accommodate the diversions. The latter caveat is important primarily to include effects of the Delta Cross Channel.

Fish adversely affected by entrainment include striped bass, delta smelt, all races of salmon, white catfish, American shad, and splittail. Some of these, particularly striped bass and delta smelt, almost certainly receive important intrinsic benefits both from outflow and by avoiding entrainment. Statistical models are inherently weak in quantifying the relative benefits of outflow and avoiding entrainment, particularly for any new physical configuration of the delta. Hence, considerable uncertainty is probably inevitable in assessing the benefits of a peripheral canal or any other water diversion facility.

Incidentally, regarding the conclusion that entrainment losses are negligible for *Neomysis*, the fact that *Neomysis* move farther off the bottom during flood tide than during ebb tide seems like an important mechanism for maintaining the location of the population in the estuary. Might that not make the population vulnerable to

1 Wim Kimmerer, BioSystems Analysis Inc. "The Peripheral Canal: What We Need to Do Before We Start Building". *Interagency Newsletter*. Autumn 1993.

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Spread and Control of Alien Smooth Cordgrass in San Francisco Bay

Donald R. Strong and Curtis C. Daehler, Bodega Marine Laboratory

Open intertidal mud without vegetation is one of the most striking features of Pacific estuaries. This contrasts with estuaries of the Atlantic and Gulf coasts, where dense tall *Spartina* cordgrasses dominate. The very character of Pacific estuarine ecology is defined by its open mud. Shore birds, some marine mammals, fish, and invertebrates, as well as flood control, recreation, and general navigation, depend on the openness of the habitat. *Spartina alterniflora*, smooth cordgrass, introduced to San Francisco Bay in the mid-1970s, is among the most aggressive, dominant, and persistent cordgrasses worldwide. This plant grows into dense, tall thickets that block the beach, cement the substrate, and exclude animals. Densely packed *S. alterniflora* stems alter marsh hydrology by hindering tidal flow and drainage. Suspended sediments precipitate, and the plants' dense root mats trap and hold sediments, rapidly raising the level of the invaded marsh. Introduced initially at New Alameda Creek in the southeast corner of the bay, the plant has spread south to San Francisco Bay National Wildlife Refuge and north along the Hayward and Alameda shores. In the west bay, *S. alterniflora* is rapidly invading mudflats north and south of the San Francisco Airport. The most recent known colonization is at Redwood Shores, near Palo Alto.

Smooth cordgrass invading San Francisco Bay grows clonally, forming large, discrete, circular patches. These circular patches show every indication of being genetic clones, each formed from a single seed or vegetative fragment (Daehler and Strong 1994). There appears to be great variation among clones in ecological characters like flowering phenology, stem size, and rate of vegetative growth. We are now developing high resolution genotypic RAPD¹ markers to distinguish individual genetic clones and trace their spread. These markers will also be useful in identifying possible hybrids between *S. alterniflora* and our native

cordgrass, *Spartina foliosa*. The native *S. foliosa* is endemic to California estuaries, growing only at the upper edge of intertidal mud. Introgression and competition with introduced *S. alterniflora* are major threats to the native *S. foliosa* in San Francisco Bay.

Our research has concentrated on understanding the biology of both introduced and native *Spartina* of the Pacific coast, with emphasis on protecting the native and controlling aliens. *S. alterniflora* experiences little in the way of interspecific competitors in Pacific marshes, so it is lacking a powerful ecological constraint upon spread. The potential for natural biological control of the alien is great in San Francisco Bay. A major insect herbivore of cordgrasses in the Atlantic, the aphid-like plant hopper *Prokelisia marginata* (Homoptera, Delphacidae; Strong *et al* 1984), occurs in San Francisco Bay, with our native *S. foliosa* its host (Daehler and Strong 1994). It feeds from the cordgrass' vascular system, through a proboscis or stylet, imbibing phloem fluid that carries carbohydrates and amides. While only modest population densities are attained by the plant hopper on the native California cordgrass, densities commonly climb to several hundred per stem and many thousands per plant on the alien *S. alterniflora* by mid-July (Daehler and Strong, *in rev*). The plant hopper also attains extraordinarily high densities on flowers of *S. alterniflora*. Numbers between 200 and 300 per inflorescence are not uncommon from July to October. In addition, we have discovered a new alien insect herbivore species, *Trigonotylus uhleri* (Homoptera, Miridae), which grows to densities of about 10 per stem and hundreds per plant in some locations on *S. alterniflora*; it is as yet rare on the native *S. foliosa*. *T. uhleri* feeds on the sap of *S. alterniflora*, leaving distinct chlorotic patches on the leaves. There is no information about how *T. uhleri*, native to the Atlantic seaboard, reached California, but its appearance demonstrates that the traffic of introduced species to

San Francisco Bay is not limited to organisms carried in ballast water.

Cordgrass inflorescences are composed of hundreds of spikelets, each of which can make a single seed. Seeds float, greatly augmenting spread of the plant, and we hypothesized that insect herbivory decreases seed set and could thereby depress spread of the weed. We found, however, that this herbivory probably does not have much depressive effect because most *S. alterniflora* clones in Pacific marshes set relatively little viable seed, even in the absence of herbivory. Substantial variation exists among clones, with a small minority of clones accounting for the lion's share of viable seed. We surmise that ovule and embryo abortion may be occurring due to inbreeding depression in this primarily out-crossing plant. We are working on pollination experiments that should allow us to establish more definitively the reason for low seed viability in most clones. We compared the viability of field-collected seed from Willapa Bay, Washington, where the plant has also been introduced, with seeds from San Francisco Bay (Figure 1). No insect herbivores of *S. alterniflora* have reached Willapa Bay, yet there was no difference in viable seed set between plants there and plants in San Francisco Bay. We have found a similar lack of direct effect of the high densities of *P. marginata* on the vegetative growth of *S. alterniflora*. We excluded most plant hoppers from selected patches in the field for 14 consecutive weeks. There was no increase in the rate of vegetative growth of these patches (Daehler and Strong, *submitted*). Greenhouse experiments with seedlings, however, demonstrate variation among clones in ability to tolerate feeding by the plant hopper.

Our most recent project is to understand an extensive die-off of *S. alterniflora* at New Alameda Creek. Several acres of the plant failed to produce new shoots in 1994, and the plants are apparently dead. With the dry winter of 1993-94, New Alameda Creek had

1 Randomly amplified polymorphic DNA.

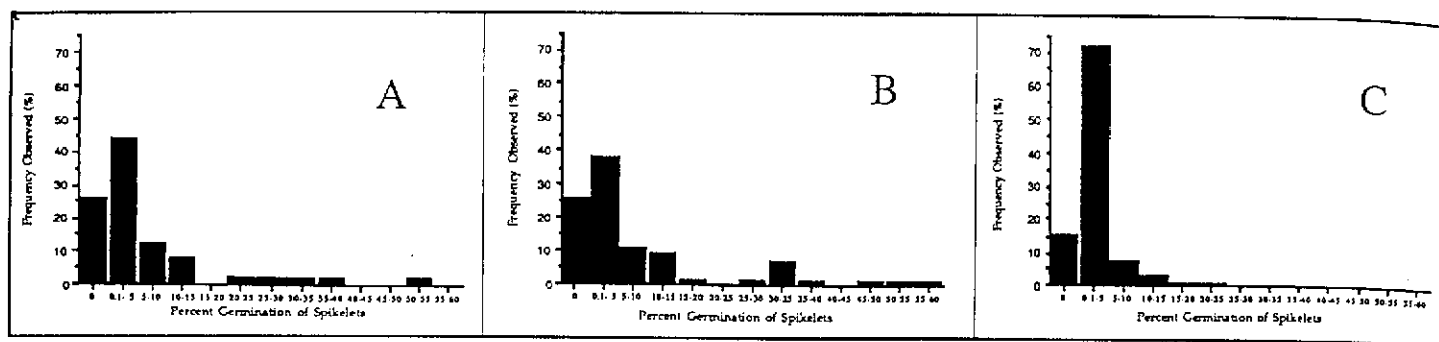


Figure 1
Frequency Distribution of Percent Spikelet Germination

A = Clones sampled from Willapa Bay, Washington, grown in the absence of herbivores (N=50).

B, C = Clones sampled from San Francisco Bay, California, herbivory by *P. marginata* [B=Coyote Hills Slough, N=72; C=San Bruno, N=97.]

Germination distributions do not differ significantly between Willapa and San Francisco bays (Kolmogorov-Smirnov 2-sample test, $P>0.2$). (From Daehler and Strong 1994)

little flow, and the stems of the previous year's growth remained *in situ* to form a thick layer of wrack. Our hypothesis is that the young shoots died due to an indirect effect of the

wrack, which can foster high densities of the plant hopper. The tide sweeps away many plant hoppers in wrack-free environments, protecting young shoots and seedlings. Although in-

vading *S. alterniflora* can tolerate high levels of herbivory under good conditions, herbivores could be a potent controlling factor under more stressful conditions.

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Summary of the Hydrodynamic Element of the Entrapment Zone Study

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Last spring the USGS hydrodynamics group, in collaboration with DWR, DFG, USBR, the USGS national research program, Tiburon Center for Environmental Studies, and Stanford University, conducted an interdisciplinary investigation of the western delta and Suisun Bay. This effort involved 2-month deployments of *in situ* hydrodynamic instrumentation during which three 30-hour synoptic investigations were conducted. The overall goal was to better understand linkages between low-salinity hydrodynamics, suspended sediment, and biology.

Specific objectives of the hydrodynamic element were to assess the relative contribution from vertical processes (eg, gravitational circulation,

strain-induced stratification, etc) on the overall salinity budget. In addition, we hoped to determine net movement, spatial extent, and interrelationships between the turbidity maximum, the null zone, and X2. This article gives an overview of the hydrodynamic data collection effort. Work is underway on a report that describes details of the experimental design, provides plots of raw and low-pass filtered (tides removed) data, and discusses preliminary results.

The hydrodynamic element involved two complementary yet distinct components. The most important component, from an analysis perspective, involved deployment of five Acoustic Doppler Current Profilers and seven self-contained submersible

Conductivity-Temperature-Depth packages along the axis of the estuary extending from Carquinez Strait to about Decker Island on the Sacramento River, as shown on the map (page 5). The equipment was deployed for about 50 days (April 11 to June 20) to capture several spring/neap cycles. In addition, the USGS toxics group (Kathy Kuivila) collected top/mid-depth Optical Back Scatter data at Mallard Island and Martinez. OBS data can be calibrated with grab samples to measure suspended solids concentration. Because time series analysis techniques can be used to "remove" the tides, the *in situ* data can be used to detect the presence or absence of gravitational circulation, the null zone, and sustained high turbidity.